University of Alberta

Systematics of *Grammia* tiger moths (Lepidoptera: Noctuidae)

by

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"Basic, descriptive work needs to return to the toolbox of modern biologists, this time augmented with a better understanding of evolutionary processes and the many technological advances that have occurred since humans first started to classify living organisms. A sentiment sometimes heard among researchers that descriptive, taxonomic work is not a true science is an expression of ignorance, forgetfulness that virtually all great biological principles and discoveries originated from countless individual observations."

Piotr Nazkrecki,
The Smaller Majority, 2005

for my family

Abstract

The genus *Grammia* Rambur (Lepidoptera: Noctuidae: Arctiinae) is revised to include 36 species, based on morphological, ecological, behavioural and molecular traits. Six species, *Grammia margo* sp. nov., *G. yukona* sp. nov., *G. brillians* sp. nov., *G. fergusoni* sp. nov., *G. yavapai* sp. nov. and *G. ursina* sp. nov. and three subspecies, *G. virguncula celineata* ssp. nov., *G. virgo gigas* ssp. nov., and *G. nevadensis vivida* ssp. nov. are described. *Grammia celia* (Saunders) is synonymized under *Grammia figurata* (Drury), and *Grammia franconia* (H. Edwards) is raised to species status. *Apantesis favorita* ab. *favoritella* Strand is revised to synonymy under *Grammia phyllira* (Drury). *Arctia speciosa* Möschler is revised to subspecies status under *Grammia virguncula* (Kirby). Adults of all species are illustrated, as well as male and female genitalia of most species. A key to all known species is provided.

Phylogenetic analysis of *Grammia* and the subtribe Arctiina (*sensu lato*) using adult morphology and molecular data revealed moderate to strong support for monophyly of the two *Grammia* subgenera. "*Grammia*" *obliterata* (Stretch), previously treated as a monotypic subgenus of *Grammia,* is congeneric with *Palearctia* Ferguson, rendering *Palearctia* a junior subjective synonym of *Holarctia* M.E. Smith. Monophyly of *Grammia* was supported only by the morphology dataset. Support for monophyly of the Arctiina *sensu lato* was weak, but a split into the subtribes Spilosomina and Arctiina (*sensu stricto*) was moderately to well supported. The subtribal classification of the North American genera previously placed in Arctiina is revised.

Sequence analysis of the mitochondrial DNA cytochrome oxidase I (*cox1*) gene proved to be of limited taxonomic value at the species level, due to extensive gene tree non-monophyly. The most parsimonious explanation for this phenomenon is taxonomically and geographically widespread introgression of mtDNA due to hybridization. This highlights the inherent dangers of drawing taxonomic conclusions based solely on mtDNA and the importance of multiple independent character sets, and also shows the value of mtDNA in detecting cryptic hybridization. Evidence for rampant mtDNA introgression was not restricted to closely related species, challenging views that interspecific gene exchange occurs rarely and that it is restricted to recently diverged species.

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The thousands of specimens examined in this study were crucial to formulating a clearer picture of *Grammia* taxonomy. I am grateful to all the museum curators and staff who facilitated specimen loans and responded to queries, including George Austin, Rob Cannings, Claudia Copley, Julian Donahue, Patricia Gentilli-Poole, Don Harvey, Don Lafontaine, Jerry Powell, Suzanne Rab-Green, and Danny Shpeley. Jocelyn Gill and David Posada kindly provided technical assistance with photography and GeoDis, respectively. The U of A "Entomology Crew" provided much helpful discussion and feedback throughout the course of my thesis, making for not only a stimulating but enjoyable work environment. I would particularly like to thank George Ball for encouraging me early on to pursue my interest in taxonomy, at a time when a project such as this seemed daunting. Rich Laffin, Lisa Lumley, Amanda Roe and Thomas Simonsen all took the time to teach me new techniques and provide feedback on my work - thank you. And perhaps most importantly, thanks to all the Entomology Grad Lounge

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Chapter 1.

General Introduction

Background

The genus *Grammia* Rambur 1866 (Lepidoptera: Noctuidae: Arctiinae) is the most speciose of northern temperate tiger moth genera, encompassing 36 species. As a result of their bright colouration, *Grammia* species have received attention from professional and amateur entomologists alike, including pioneers of taxonomy and entomology such as Carolus Linnaeus and Dru Drury, their authorship of four species epithets bearing testament to this. Due to their popularity, coupled with subtle interspecific variation and often considerable within-species variability, the majority of the 84 names proposed for the 25 valid species (as defined here) recognized prior to 1985 apply to variants and subspecies. The majority of *Grammia* names were proposed by A.R. Grote, B. Neumögen, H. Strecker, and R. H. Stretch, all of whom figure prominently in the nomenclature of North American moths.

The species of *Grammia* were revised by Marion Smith (1938a), whose work also included species now placed in the genera *Apantesis* Harris and *Notarctia* M.E. Smith. Smith's work was unfortunately published only as a 12 page abstract (Smith 1938b). Smith was the first to recognize the natural groups of taxa that would eventually be segregated into separate genera, although not for nearly another 50 years (Ferguson 1985). Smith's revision of the group was based largely on larval, pupal, and external genitalic characters, prior works having relied entirely on wing markings. Shortly after Smith's work, Eugene Munroe (1941) summarized *Grammia, Notarctia* and *Apantesis* (as *Callarctia* Packard and *Apantesis*) in an unpublished M.Sc. thesis, wherein he retained the genera and subgenera proposed by Smith (1938a,b), and further grouped the subgenus *Grammia* (as *Callarctia*) into three species groups based on wing pattern. The generic (and subgeneric) classification proposed by Smith and Munroe were not adopted by Forbes (1960) or Franclemont (1983).

Although Smith (1938a) recognized the importance of morphology in delineating subgenera and genera in the *Grammia-Apantesis-Notarctia* group, she also noted the paucity of morphological variation among species and species groups. The conserved genitalic morphology in *Grammia* has been a significant impediment to the taxonomy of this group, compounded by the rarity of many western species. The discovery of additional morphological characters (Ferguson & Schmidt 2007, Chapter 2), coupled with the availability of much additional museum material, has however provided a much-improved taxonomic resolution of this group. As discussed in Chapters 2 and 3, the taxonomic utility of molecular data (cytochrome oxidase I gene) has proven to be minimal, and in fact points to a significant decoupling of genomic integrity from mitochondrial DNA genealogy (Chapter 3).

Grammia biology

Nearly all (35/36) species of *Grammia* occur in North America, with only one species (*G. kodara* Dubatolov & Schmidt) restricted to the Palaearctic, and two species (*G. quenseli* Paykull and *G. philipiana* Ferguson) occurring in both the Palaearctic and Nearctic regions. The genus reaches its greatest diversity in the grasslands of the Great Plains and the southern Rocky Mountain region, although the genus has a transcontinental distribution, occurring from the Arctic coast to central Mexico. Dry, sparsely vegetated biomes are preferred *Grammia* habitats, including tundra, open forest, rocky slopes, grasslands, sand dunes and gravelly or rocky substrates.

Since *Grammia* species rarely reach high population densities and are generally not important from an economic perspective, detailed knowledge of their life history remains fragmentary. Notable exceptions to this are *G. blakei* (Grote) and *G. incorrupta* (Hy. Edwards). *Grammia blakei* larvae can occasionally reach densities high enough to cause minor damage to spring crops in the northern Great Plains, and aspects of *G. blakei's* biology were therefore published by Byers (1988, 1989). The ecology of *G. incorrupta* larvae has received considerable attention (e.g. Singer 2001, Singer and Stireman 2001, 2003, Bernays and Singer 2005) in light of herbivory patterns and interactions between plant compounds and larval parasitoids, stemming from the work of Singer (2000).

Little is known about the reproductive ecology of *Grammia*. Use of female pheromones in mate attraction has been documented in *G. blakei* (Byers 1988) and *G. arge* (Conner et al. 1985), and this is presumably the norm for the genus. Conner et al. (1985) describe the rhythmic pulsing of the abdomen in *G. arge* during pheromone emission, behaviour that is similar to other members of the tribe (Conner et al. 1985, BCS personal obs.). Onset of calling behaviour in *G. arge* occurs about 5.5h after dark (Conner et al. 1985). The female pheromone gland is located dorsally between abdominal segments 8 and 9, and pulsing of the abdomen is associated with expulsion of liquid pheromones from this gland (Bendib & Minet 1998). It is not known if male pheromones exist in *Grammia*, and if these play a role in courtship. The complex coremata (pheromone-dispersing structures) and courtship behaviour of other arctiine species (reviewed by Weller et al. 1999) are highly reduced in *Grammia*, and do not appear to be functional. The chemical precursors associated with male pheromones in other arctiids, hydroxydanaidal, is absent in *G. incorrupta* (Hartmann et al. 2005). Similarly, the microtymbals (sound-producing structures used in acoustic aposematism and courtship [Weller et al. 1999]) are simplified in *Grammia*, but are still functional (Fullard and Fenton 1977). Absence of the tymbal microstriae appears to be a secondary loss rather than a primitive character (Weller et al. 1999)

Females lay between several hundred and a thousand eggs; these lack adhesive, and are laid haphazardly among ground litter (Singer 2000). Fully gravid females are likely very poor fliers, and eggs are laid while the females are on the ground (Singer 2000). Larvae are highly polyphagous on herbaceous plants, but prefer dicots; *G. incorrupta* feeds on over 80 plant species in 50 families under natural conditions, regularly changing host species throughout the course of a single day (Singer 2000). Parasitism of larvae by tachinid flies and hymenopterans has been shown to induce a preference for plants containing pyrolizidine alkaloids (Bernays and Singer 2005), compounds which are detrimental to the parasitoid (Singer and Stireman 2003), and as such the larvae are able to self-medicate when parasitized. *Grammia incorrupta* possesses the ability to detoxify and store all types of pyrolizidine alkaloids occurring in its environment (Hartmann et al. 2005), a process mediated by an enzyme thought to be present in the ancestor of the Arctiini (Weller et al. 1999). Like many other arctiines studied to date, larval *Grammia incorrupta* are able to convert and store plant-derived pyrolizidine alkaloids, conferring chemical protection to the adult stage (Hartmann et al. 2005).

Adults of *Grammia* are relatively short lived (1 – 3 weeks, Singer 2000) since mouthparts are non-functional. In contrast, larvae tend to be relatively long-lived since they overwinter in the mid- to late instars (Byers 1988, Singer 2000). Instar number is variable in *G. incorrupta*, generally with seven or eight instars, but with as many as 12 (Singer 2000). *Grammia blakei* larvae go through seven instars (Byers 1988). Although most *Grammia* species undergo a single generation per year, some species (e.g. *G. incorrupta, G. arge, G. figurata*; Chapter 2) have multiple yearly broods. Pupation occurs in or near the soil surface amongst debris or loose soil in a flimsy cocoon (Byers 1988, Singer 2000, BCS pers. obs.). The dense setation and high motility of larvae functions to escape predation from invertebrates such as ants, ground beetles and wasps (Singer 2000), and the highest larval mortality is due to parasitism by tachinid flies (Singer 2000, Stireman and Singer 2002). Larvae actively feed during the day, seeking shelter during the hottest hours, and much time is spent resting on the ground (Singer 2000, BCS pers. obs.).

Thesis overview

A taxonomic revision of the genus *Grammia*, based on adult morphology, ecology, behaviour, biogeography and molecular sequence data is given in Chapter 2. The genus is revised to include 36 species, and 14 subspecies are recognized. Six species are described as new, *Grammia margo* sp. nov., *G. yukona* sp. nov., *G. brillians* sp. nov., *G. fergusoni* sp. nov., *G. yavapai* sp. nov. and *G. ursina* sp. nov. Two of these, *G. margo* and *ursina*, are cryptic species that have previously gone unrecognized. The remaining four species have come to light relatively recently (i.e. within the past 20 - 30 years), are rarely collected, and have restricted distributions. Three new subspecies are proposed, and neotypes are designated for four taxa. Lectotypes are designated for five taxa. One taxon is raised to specific status, and two specific names are revised to junior synonyms. "*Grammia*" (subgenus *Holarctia*) *obliterata* is transferred from the genus *Grammia* to the genus previously recognized as *Palearctia* Ferguson, for which the genus-group name *Holarctia* Smith has priority.

Molecular sequence data of the mtDNA *cox1* gene proved to be of limited taxonomic value, because even morphologically divergent species exhibited shared or similar (<0.5% divergence) haplotypes. With the exception of nine haplotype lineages that were consistent with species concepts based on all other taxonomic characters, mtDNA paraphyly was extensive. This significant discrepancy between morphological / biological cohesiveness and mtDNA is examined in detail in Chapter 3. There, I argue that the most plausible explanation for non-monophyly is geographically widespread mtDNA introgression through hybridization events. This interpretation is supported by the correlation between genetic and geographic structuring, biogeography, and *Grammia* biology and nested clade analysis. These results show that the commonly held view of hybridization being extremely rare or unnatural, particularly among relatively distantly related species, warrants serious reconsideration, and also that gene flow across species boundaries may be an important aspect of evolution.

In Chapter 4, I investigate the phylogenetic placement of *Grammia* within the Arctiini. Previous work has shown conflicting interpretations of relationships among generic groupings and subtribes in relation to *Grammia*. Phylogenetic analysis of 24 ingroup and 7 outgroup genera, using adult morphology (81 characters) and *cox1* molecular data (658 bp), supports the recognition of two subtribes, Spilosomina and Arctiina, for the genera that have variously been grouped as one, two or three subtribes. Several novel synapomorphies for these subtribes are proposed, and subtribal membership for the North American taxa previously treated as Arctiina is revised. Previously proposed subtribal and generic groupings that included *Grammia* were not recovered as monophyletic.

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Chapter 2.

Taxonomic revision of the genus *Grammia* Rambur (Lepidoptera: Noctuidae: Arctiinae)

INTRODUCTION

Grammia Rambur 1866 (Noctuidae: Arctiinae) is the largest genus of northern temperate tiger moths, here revised to include 36 species. Nearly all *Grammia* species are restricted to the Nearctic region, with two species occurring in both the Nearctic and Palaearctic (Dubatolov 2003, Ferguson 1985), and one species known only from the Palaearctic (Dubatolov & Schmidt 2005). Because of their bright, attractive colouration, *Grammia* have received attention from both amateur and professional entomologists, resulting in a long history in the literature. Despite their popularity, *Grammia* species can be notoriously difficult to identify, as a result of often considerable intraspecific variation, conservative variation in genitalic morphology, and similar wing pattern and colour among species-groups and even between *Grammia* and closely related genera such as *Holoarctia* Ferguson and *Holarctia* Smith (Ferguson 1985).

The highest diversity of *Grammia* species occurs in western North America, primarily in xeric grasslands and open wooded habitats. Although most western species occur at low elevations, several species occur only in alpine and arctic habitats. Relatively few species have distributions exclusive to eastern North America, but these species are again often associated with dry, open forest habitats such as oak / pine barrens and poor or shallow soils such as sand hills, beaches and limestone alvars (Handfield 1999). A few species are common in mesic and wetland habitats. Unlike many other Arctiinae, *Grammia* larvae are not host-specific, and feed on a wide variety of low-growing dicots, as well as grasses and sedges on occasion (Singer 2000). Despite the lack of larval host specificity, many species are very local in occurence, likely limited by microhabitat variables such as vegetation cover and soil substrate type. The dark-coloured, densely setose larvae, which feed on low-growing plants, exhibit typical adaptations to cold, arctic and alpine environments, and are one of only a few arctiine genera to occur in arctic-alpine habitats (Ferguson 1985).

Traditionally placed within the subfamily Arctiinae (Noctuoidea: Arctiidae), *Grammia* is one of several closely related genera largely restricted to the temperate regions of the Nearctic and Palaearctic. Recent advances in the classification and phylogeny of the superfamily Noctuoidea have resulted in an expanded concept of the family Noctuidae, which includes previous concepts of the Arctiidae as the subfamily Arctiinae (Lafontaine and Fibiger 2006), and I follow the classification proposed therein. Within the Arctiinae (*sensu* Lafontaine and Fibiger 2006), *Grammia* are currently placed in the tribe Arctiini, subtribe Arctiina (Franclemont 1983, Ferguson 1985, Ferguson and Opler 2006), or subtribe Micrarctiina (Dubatolov 1996, 2003). Jacobson and Weller (2002) did not resolve the Arctiina as monophyletic in their study of morphological characters of immatures. *Grammia* appears to be most closely related to the nearctic genera *Apantesis* Harris, *Notarctia* Smith and *Holarctia* Smith, all of which have vein R_1 of the forewing arising before the distal end of the discal cell (Fig. 2-1d, Ferguson 1985). Members of the genera *Chelis* Rambur, *Hyperborea* Grum-Grshimailo, *Neoarctia* Ferguson, and *Holoarctia* Ferguson can be very similar in wing markings and colouration, but are more distantly related to *Grammia* than *Notarctia* and *Apantesis* (Chapter 4). Morphological characters defining the genus *Grammia* include an undivided, flat and slightly concave male valve which is usually broadly rounded, occasionally spatulate or crescentic; juxta lacking spinules and approximately as wide as long; uncus simple, with a broad base and and abrupt constriction defining apical portion; aedeagus short and stout, lacking apical spinules or cornuti, apical opening of aedeagus directed right laterad; vesica with three poorly differentiated, spherical or kidney-shaped chambers; highly reduced coremata with stout, minute corematal setae. The female genitalia exhibit a ductus bursae that is unsclerotized basally; bursae copulatrix spherical or pear-shaped, with four signa; ductus seminalis swollen and coiled proximally, but distinctly smaller than corpus bursa. Although the wing pattern is highly variable, it is based on a 'groundplan' pattern unique to *Grammia*, as discussed by Ferguson (1985).

Taxonomic history of *Grammia*

The first *Grammia* species to be named was *Bombyx virgo*, by Carolus Linnaeus in his seminal *Systema Naturae* (1758), and some species were well known to other early authors including Drury, Fabricius, and Hübner. Nearly all currently valid *Grammia* species names were proposed prior to 1900 (excluding the names proposed herein). The genus was revised by Marion Smith (1938a), but aside from a 12 page abstract (Smith 1938b), this thesis was unfortunately never published. Smith (1938a) recognized 22 species of *Grammia* compared to the 24 species listed shortly prior to her revision in McDunnough's "Check List of the Lepidoptera of Canada and the United States" (McDunnough 1938). Five taxa treated as species by McDunnough (1938) were informally synonymized by Smith (*Arctia quadranotata* Strecker, *Apantesis gibsoni* McDunnough, *Arctia elongata* Stretch, *Arctia intermedia* Stretch, *Arctia oithona* Strecker), while three taxa were raised to species status (*Arctia quenselii* ab. *complicata* Walker, *Arctia edwardsii* Stretch and *Apantesis ornata hewletti* Barnes and McDunnough). Smith (1938a) did not describe any species as new, but, more importantly, provided the genus-group names *Holarctia* and *Notarctia*. To this end, Smith's (1938a) most significant contribution to the taxonomy of the *Grammia* group of genera was based on the structural characters of the larvae, pupae and adult genitalia, reflected in the modern concepts of the two subgenera of *Grammia* (*Mimarctia* and *Grammia*), *Apantesis*, *Notarctia* and *Holarctia* (Table 2-1). Shortly after Smith's work, Eugene Munroe summarized *Grammia*, *Notarctia* and *Apantesis* (as *Callarctia* and *Apantesis*) in an unpublished M.Sc. thesis (Munroe 1941); Munroe proposed no taxonomic changes, maintaining the genera and subgenera proposed by Smith (1938a, b), and further divided the subgenus *Grammia* (as *Callarctia*) into three species groups, based on wing pattern.

The generic (and subgeneric) treatments proposed by Smith and Munroe were not adopted by Forbes (1960) or Franclemont (1983), both of whom included under *Apantesis* all species under the current concepts of *Grammia*, *Notarctia* and *Apantesis* (Table 2-1). The current generic arrangement follows that proposed by Ferguson (1985), who was the first to apply the name *Grammia* to North American taxa, following Inoue *et al.* (1982) who applied *Grammia* to *G. quenseli* (Paykull). Prior to Smith (1938a), Hampson (1901) included all three current genera (*Grammia, Notarctia* and *Apantesis*) under *Apantesis* (an arrangement followed by McDunnough [1938], Table 2-1), in addition to *Arctia fasciata*. Similarly, Neumögen and Dyar (1894) were the first to unite all *Grammia*-group species in one genus, *Euprepia*, with five constituent subgeneric groups, based on wing pattern. The species groups of Neumögen & Dyar (1894) partially corresponded to the groups subsequently defined by Smith (1938a) based on internal morphology (Table 2-1).

Due to the paucity of morphological characters traditionally used to delineate species, and the relatively large number of species available for sampling, *Grammia* is an ideal candidate group to test the utility of species-level molecular taxonomy. Mitochondrial DNA nucleotide sequence data has proven useful in resolving species problems by providing additional characters with which to assess species delimitations (Simon *et al.* 1994, Caterino *et al.* 2000), particularly the cytochrome-c oxidase gene regions I and II (*cox1, cox2*) in Lepidoptera (Caterino *et al.* 2000, Sperling 2003a). The species-level diagnostic power of *cox1* has resulted in "DNA barcoding" initiatives across a wide range of animal taxa (Hebert *et al.* 2003), although not without its limitations (Lipscomb *et al.* 2003, Sperling 2003b, Will and Rubinoff 2004, Gompert *et al.* 2006, Chapter 3). The purpose of this study was to revise the species-level taxonomy of *Grammia* using a 'total evidence' approach by combining morphology, wing pattern, ecology, biogeography and *cox1* sequence data. Although genitalic morphology in *Grammia* has been of limited use in discriminating closely-related species (Smith 1938a), prior study has largely been limited to external male genitalia. Here, I expand the morphological character set to include the everted male vesica, female genitalia, and eye and antennal structure. The genus is revised to include 36 species, including 14 subspecies. One additional species, *Holarctia obliterata* (Stretch) is also included here, since it has previously been treated as congeneric with *Grammia* (Chapter 4). Six species are described as new, *Grammia margo* sp. nov., *G. yukona* sp. nov., *G. brillians* sp. nov., *G. fergusoni* sp. nov., *G. yavapai* sp. nov. and *G. ursina* sp. nov. Three new subspecies are proposed, *G. virguncula celineata* ssp. nov., *G. virgo gigas* ssp. nov., and *G. nevadensis vivida* ssp. nov. Neotypes are designated for *Callimorpha parthenice* Kirby, *Callimorpha virguncula* Kirby, *Arctia williamsii* Dodge, and *Arctia edwardsii* Stretch. Lectotypes are designated for *Arctia speciosa* Möschler, *Arctia quadranotata* Strecker, *Arctia oithona* Strecker, *Arctia incorrupta* Hy. Edwards, *Apantesis tooele* Barnes and McDunnough, and *Arctia favorita* Neumögen. *Arctia celia* Saunders is revised to synonymy under *Grammia figurata* (Drury), and *Grammia franconia* (H. Edwards) is raised to species status. *Apantesis favorita* ab. *favoritella* Strand is revised to synonymy under *Grammia phyllira* (Drury). *Arctia speciosa* Möschler is revised to subspecies status under *Grammia virguncula* (Kirby).

METHODS AND MATERIALS

Morphological techniques

Adult genitalia were prepared following the methods detailed by Lafontaine (2004). Cleaned, stained genitalia were mounted in Canada Balsam, and photographed using a Nikon Coolpix 900 digital camera mounted to a dissecting microscope. Multiple-focus images of each preparation were composed in AutoMontage (Syncroscopy, Frederick, MD), and subsequently edited in Adobe Photoshop CS. Photographs of adult moths were taken under natural light conditions, and edited in Adobe Photoshop CS, including digital repairs where necessary, with the exception of holotypes, neotypes and lectotypes. Nomenclature of genitalic morphology primarily follows that of Goater *et al.* (2003), who provide genitalic terminology for the Catocalinae (Noctuidae), which are thought to be relatively closely related to the Arctiinae (e.g. Lafontaine & Fibiger 2006). Wing pattern nomenclature follows that of Ferguson (1985); it is important to note that similar wing pattern terminology does not neccessarily indicate homologies in other Noctuoidea, but the terms are used here for the sake of convenience. Forewing length measurements were taken with calipers accurate to the nearest 0.1 mm. Eye and antennal measurements were taken with a Wild dissecting microscope at 50x magnification, accurate to the nearest 0.02 mm.

Specimens examined

Approximately 25,000 specimens were examined, primarily those of the following collections: CNC, USNM, UASM, UCB, UCD, JTT, LACM, RBCM and MCG. Abbreviations for collections used throughout are as follows:

AMNH: American Museum of Natural History, New York
ANSP: Academy of Natural Sciences, Philadelphia, Pennsylvania
BCSC: B. Christian Schmidt Personal Collection, Ottawa, Ontario
BMNH: The Natural History Museum (formerly British Museum [Natural History]), London
CAS: California Academy of Sciences, San Francisco, California.
CNC: Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Ontario
CU: Cornell University, Ithaca, New York
CSU: C.P. Gillette Arthropod Biodiversity Museum, Colorado State University, Colorado
LACM: Los Angeles County Museum of Natural History, Los Angeles, California
MCG: McGuire Center for Lepidoptera and Biodiversity, Gainesville, Florida
MCZ: Museum of Comparative Zoology, Cambridge, Massachusetts
RBCM: Royal British Columbia Museum, Victoria, British Columbia
UASM: University of Alberta Strickland Entomological Museum, Edmonton, Alberta
UCB: Essig Museum of Entomology, University of California, Berkeley, California
UCD: Bohart Museum of Entomology, University of California, Davis, California
USNM: National Museum of Natural History (formerly United States National Museum), Washington, DC
ZIN: Zoological Institute, St. Petersburg, Russian Federation.
ZMHU: Zoologisches Museum, Humboldt Universität, Berlin
ZMUM: Zoological Museum, Moscow State University, Moscow

In addition to museum material, specimens were obtained through field collections carried out in western Canada, particularly to target rare and taxonomically difficult species for fresh material suitable for DNA extraction. Adult moths were trapped with UV light traps or hand-netted, and freshly killed specimens or legs thereof were frozen at –20 °C or –70°C, or were placed in 99% ethanol prior to storage at –70°C if freezer facilities were not immediately available. Voucher material is deposited in the UASM and CNC. Voucher data for genitalic preparations, illustrations, and additional mtDNA sources are given in Appendix 2-1. Distribution maps of examined material were compiled using DIVA-GIS 5.0. Geographic co-ordinates of collection localities were referenced using GEOLocate (Rios and Bart 2004), Placenames.com, and the Canadian Geographical Names Data Base (Natural Resources Canada, 2006). Standard postal abbreviations for Canadian provinces and American states are used here.

Molecular techniques

Molecular variation within the genus *Grammia* was assessed based on the 658 bp 'barcode' region of the first subunit of the cytochrome oxidase (*cox1*) gene (Hebert *et al.* 2003), corresponding to nucleotide positions 1490–2198 of the *Drosophila yakuba* mitochondrial genome (Clary and Wolstenholme 1985). One to two legs of dried or fresh frozen specimens were sent to the University of Guelph in dry Eppendorf tubes, and processed as part of the "All Leps Barcode of Life Campaign" (www.lepbarcoding.org). Recently collected specimens (0 - 10 yr) suitable for DNA extraction were obtained through field work carried out in western Canada, particularly in Alberta, but also in British Columbia and the Yukon. A significant proportion of sequenced samples were made available by private collectors and collaborators, either as donated specimens or as DNA sequences through the All Leps Barcode of Life Campaign (Appendix 2-1). DNA extraction, amplification and sequencing protocols for the Barcode of Life initiative are detailed in Hebert *et al.* (2003).

In addition to the *cox1* barcode region, a subsample of 36 specimens representing 19 species was sequenced for the 770 bp region of *cox1* adjacent to the barcode region, using the primer pair 'Jerry' (CAACATTTATTTTGATTTTTTGG; C1-J-2183 of Simon et al. 1994) and 'Pat II' (TCCATTACATATAATCTGCCATATTAG; L2-N-3014 of Simon et al. 1994). Genomic DNA was extracted from legs of specimens using the QIAamp DNA Mini Kit (250) (Qiagen, Valencia, CA), and amplified through the Polymerase Chain Reaction (PCR) with heterologous primer pairs on either a Whatman Biometra TGradient or TPersonal Thermocycler (Whatman Biometra, Göttingen, Germany), with an initial denaturation cycle at 94°C for 2 min, followed by 35 cycles of 94°C for 30 s, 45°C for 30 s, 72°C for 2 min, and a final extension at 72°C for 5 min. PCR products were cleaned using a QIAquick PCR Purification Kit (250) (Qiagen, Valencia, CA) and cycle-sequenced on either a Whatman Biometra TGradient or TPersonal Thermocycler using Amersham Bioscience DYEnamic ET Dye Terminator Kit (Amersham Biosciences, Buckinghamshire, England) according to the following profile: initial denaturation at 93.0°C for 30 s, 28 cycles of 95°C for 20 s, 45°C for 15 s, 60°C for 1 min, with a final extension at 60°C for 30 s. The sequenced product was purified through filtration with Sephadex columns (Amersham Biosciences, Uppsala, Sweden) and subsequently dried, then re-suspended in formamide and sequenced on an ABI 377 automated sequencer (Applied Biosystems, Foster City, CA). All fragments were sequenced in both directions and manually aligned using Sequencher 4.1 (Gene Codes Corp. 2001). Extracted DNA is stored at the Strickland Entomological Museum, University of Alberta, Edmonton, Alberta.

Sampling of non-molecular characters

Fourty-three non-molecular characters were established for phylogenetic analysis, consisting of 22 wing pattern/colour and vestiture colour characters, 10 genitalic characters, six larval/pupal morphology characters, two antennal morphology characters, and two behavioural characters (attraction to light) (Appendix 2-2). Wing phenotype characters were chosen to represent those that showed little to no intraspecfic variation, based on examination of all available study material from multiple geographic regions representative of a species' range. Wing phenotype characters proved to be much more character-rich than genitalic morphology, which is highly conserved within the genus. Larval and pupal morphology characters are based on Smith (1938a), Forbes (1960), and

Ferguson (1985), and were indepedently assessed where possible. All characters were coded as binary and treated as unordered.

Phylogenetic analysis

Haplotypes of all *cox1* fragments were initially compared for the 227 sampled individuals with phylograms constructed using the neighbour-joining method in PAUP 4.0*b10 (Altivec) (Swofford 2002). Phyletic distances were calculated using the Kimura-2-Parameter (K2P) distance model. Phylogenies using non-molecular, *cox1* and combined data sets were estimated using maximum parsimony (MP) phylogenetic analysis implemented in PAUP 4.0*b10 (Altivec) (Swofford 2002), using heuristic searches with the following parameters: 100 random addition replicates; stepwise addition; tree bisection-reconnection (TBR). Branch support was calculated using bootstrap support values, obtained through 100 bootstrap replicates using the heuristic search methods given above. Character states for internal nodes were assigned using accelerated transformation (ACCTRAN) optimization in PAUP. *Notarctia proxima* (Guérin-Méneville) and *Apantesis phalerata* (Harris) were chosen as outgroup taxa, since these genera are believed to be the sister group to *Grammia* (Ferguson 1985).

Maximum parsimony analysis of the 'barcode' data set was conducted on a subsample of the total sequenced specimen database. For species with non-overlapping haplotype clusters (as determined by the neighbour-joining analysis), up to three representative haplotypes per species were used, chosen to represent the largest divergences within a haplotype cluster. For Western and Eastern lineage haplotypes, the high degree of haplotype sharing and/or similarity among species (see "Results" section) made it impractical to subsample haplotypes of all species. For these lineages, the haplotype subsamples were therefore chosen to represent the largest divergences within a lineage, regardless of taxonomy. The number of subsampled haplotypes was arbitrarily set at nine.

Species concepts

Delimiting species within a group as diverse and taxonomically complex as *Grammia* warrants some discussion of species concepts. The fundamental problem of how to define a species has given rise to a wealth of literature, discussion, and often controversy, and not surprisingly an equally rich array of definitions; Coyne and Orr (2004) list more than 25 different published species concepts. Although there is an overall lack of consensus among biologists for a single species concept, a pragmatic solution to understanding and defining species can be attained by combining the strengths of multiple concepts. To this end, the genomic integrity definition of Sperling (2003) provides a more practicable solution to the popular biological species concept (BSC; Mayr 1963) by addressing two major drawbacks of the BSC, the problem of allopatry and introgression/hybridization as discussed by Coyne and Orr (2004). The genomic integrity species definition states that species consist of populations that maintain their genomic integrity when they contact each other (despite possible occasional gene exchange), or allopatric populations that exhibit genetic divergences equivalent to that occuring in comparable sister species in sympatry or parapatry (Sperling 2003a). As discussed below and in Chapter 3, the extensive mtDNA polyphyly among most *Grammia* species presents not only an interesting case study in species delimitation, but also a case where genomic integrity and mtDNA heritability are decoupled. Contrary to the extensive polyphyletic patterns of mtDNA phylogeny, the genomic integrity as measured by morphological, ecological and behavioural divergences clearly delineate sympatric and parapatric species that share identical or very similar mtDNA sequences. This pattern of polyphyly not only necessitates a species concept that accomodates interspecific gene flow, but also challenges conventional species concepts by demonstrating frequent or ongoing gene introgression across distantly related, sympatric congeners. Where possible, I have therefore emphasized morphological and ecological differences among sister taxa, rather than relying on molecular data. The significant pitfalls of limited specimen and species sampling among polyphyletic DNA lineages are discussed by Funk (1999).

In general, I have avoided use of subspecies designations to avoid potentially unwarranted taxonomic changes for species where data on intraspecific variation (both molecular and non-molecular) is inadequate, particularly in light of the complex mtDNA genealogy of *Grammia* species (Chapter 3). However, in several cases I felt it was prudent to recognize subspecies based on the available evidence, consisting of geographically structured phenotypic variation concordant with variation in *cox1* sequence. Although use of subspecies designations has been debated and often criticized (see for example Vanzolini 1992 and Ehrlich 2000), geographically structured, intraspecific variation plays an important role in the evolutionary legacy of species (Avise and Ball 1990). Avise and Ball (1990) provide a useful framework for defining subspecies: "Subspecies are groups of actually or potentially interbreeding populations, phylogenetically distinguishable from, but reproductively compatible with, other such groups. Importantly, the evidence for phylogenetic distinction must normally come from concordant distributions of multiple, independent, genetically based traits." To this end, I feel that recognition of *Grammia* subspecies is warranted in several cases, discussed further in the species accounts.

SYSTEMATIC ACCOUNT

Overview

The phylogenetic results are discussed in detail at the end of this chapter, following the systematic account section. To provide a framework for the species accounts that follow, a brief overview of the phylogenetic results and their implications is provided here. Analysis of molecular and non-molecular data has three important ramifications for the systematics of *Grammia*: 1) the subgenera *Mimarctia* (consisting of *G. arge* and *G. doris*) and *Grammia* (consisting of the remaining 34 species) are moderately to well supported as natural groups, and subgenus usage is therefore maintained herein. 2) Morphological and molecular data show that *"Grammia" obliterata* is not congeneric with *Grammia*, and this species is transferred to *Palearctia* Ferguson, for which the name *Holarctia* M.E. Smith has priority. Although a review of the genus *Holarctia* is beyond the scope of this revision, a synopsis of *Holarctia obliterata* is given since it has previously been included in *Grammia*. 3) Molecular and non-molecular phylogenies show significant discrepancies in delimiting most species. As discussed in Chapter 3, the most parsimonious explanation for these discrepancies is taxonomically and geographically widespread introgression of mtDNA resulting from hybridization events. Since the genotypic variation of many *Grammia* species seems to unequivocally point to hybridization between species that are not closely related (as defined by morphology, phenotype, ecology and biogeography), non-molecular traits delimiting species are provided in the 'Diagnosis' section. As such, this section serves as an identification guide and as justification for recognizing species limits. The order in which species are discussed below reflects approximate phylogenetic relationships, as previous arrangements (Franclemont 1983, Ferguson & Opler 2006) are for the most part artificial.

CHECKLIST OF *GRAMMIA* SPECIES

SUBGENUS *MIMARCTIA* NEUMÖGEN & DYAR

1. *Grammia arge*
2. *Grammia doris*
    2a. *G. d. doris*
    2b. *G. d. minea*

SUBGENUS *GRAMMIA* RAMBUR

3. *Grammia phyllira*
4. *Grammia placentia*
5. *Grammia virgo*
    5a. *G. v. virgo*
    5b. *G. v. gigas* **ssp. nov.**
6. *Grammia anna*
7. *Grammia parthenice*
8. *Grammia virguncula*
    8a. *G. v. virguncula*
    8b. *G. v. speciosa*
    8c. *G. v. celineata* **ssp. nov.**
9. *Grammia kodara*
10. *Grammia philipiana*
11. *Grammia quenseli*
12. *Grammia margo* **sp. nov.**
13. *Grammia franconia* **stat. rev.**
14. *Grammia figurata*
15. *Grammia f-pallida*
16. *Grammia incorupta*
17. *Grammia allectans*
18. *Grammia ursina* **sp. nov.**
19. *Grammia nevadensis*
    19a. *G. n. nevadensis*
    19b. *G. n. superba*
    19c. *G. n. geneura*
    19d. *G. n. gibsoni*
    19e. *G. n. vivida* **ssp. nov.**
20. *Grammia yukona* **sp. nov.**
21. *Grammia behrii*
22. *Grammia brillians* **sp. nov.**
23. *Grammia fergusoni* **sp. nov.**
24. *Grammia bolanderi*
25. *Grammia williamsii*
    25a. *G. w. williamsii*
    25b. *G. w. tooele*
26. *Grammia favorita*
27. *Grammia elongata*
28. *Grammia yavapai* **sp. nov.**
29. *Grammia bowmani*
30. *Grammia blakei*
31. *Grammia cervinoides*
32. *Grammia ornata*
33. *Grammia hewletti* **stat. rev.**
34. *Grammia complicata*
35. *Grammia edwardsii*
36. *Grammia eureka*

KEY TO *GRAMMIA* SPECIES

1.

Distal half of forewing with at least some pale vein lines (*e.g.* Fig. 2-6b, 2-8, 2-9, 2-36)…**2**

Distal half of forewing completely lacking pale vein lines (*e.g.* Fig. 2-6a, 2-7, 2-19, 2-32, 2-34)…**18**

2.

Forewing costal area with broad, pale stripe between costa and R+M vein, extending to wing apex or nearly so (Figs. 2-4, 2-5)…**3**

Forewing costal area without pale stripe (*e.g.* Figs. 2-3, 2-8, 2-9, 2-10), or with a pale line limited to costal vein, not expanded into costal space…**4**

3.

Hindwing pinkish white, with postmedial dark spots pale-lined along veins (Fig. 2-4); costal part of subterminal and anal part of postmedial forewing bands forming nearly a straight line (Fig. 2-4); pale forewing bands expanded so that dark areas are generally smaller than pale areas; apex of valve broad and rounded (Fig. 2-40a)…***G. arge***

Hindwing deep pink, with postmedial dark spots entire (Fig. 2-5); costal part of subterminal and anal part of postmedial forewing bands forming distinct angle (>20°) (Fig. 2-5); pale forewing bands not expanded, area of dark portions greater than pale portions; apex of valve narrow and crescentic (Fig. 2-41a)…***G. doris***

4.

Transverse banding pattern restricted to ST ('zig-zag') band, AM, medial and postmedial bands absent (*e.g.* Figs. 2-11a,b,c,d)...**5**

Transverse banding pattern with AM, medial or postmedial bands (*e.g.* Figs. 2-8, 2-9,2-10) or fragments thereof, sometimes only at costal margin (Fig. 2-3) or in discal cell (Figs. 2-12, 2-14, 2-11f, 2-11g)...**7**

5.

Hindwing orange (Fig. 2-13); eyes strongly reduced and ellipsoid; Alaska, Yukon, and far eastern Siberia only...***G. philipiana***

Hindwing yellow, greyish-yellow or grey (Figs. 2-11c,f,g, 2-14); eyes reduced or normal...**6**

6.

Eyes reduced and ellipsoid (< 0.60 mm diameter); scales of antennal shaft predominantly pale buff; hindwing predominantly greyish, dark markings obscure (Fig. 2-14)...***G. quenseli*** (in part)

Eyes spherical, not reduced and ellipsoid (> 0.60 mm diameter); antennal scales predominantly or entirely black; hindwing yellow with well-defined black markings, although often confluent...***G. virguncula*** (in part)

7.

Hindwing lacking all of the following: a) antemedial spots, b) basal dark streaks and c) black markings along anal margin (Fig. 2-3, 2-6, 2-10)...**8**

Hindwing with at least one of the following: a) antemedial spots (Fig. 2-8, 2-9), b) basal dark streaks (Fig. 2-11a), c) black markings along anal margin (Fig. 2-9)...**10**

8.

Forewing postmedial band not extending beyond medial vein (Fig. 2-3); valve apex sharply pointed, short (Fig. 2-42a); corpus bursae with 3 signa (Fig. 2-74)... ***Holarctia obliterata***

Forewing postmedial band extending beyond medial vein, reaching to or beyond postcubital stripe (Fig. 2-6b,c, 2-10); valve apex rounded and flat (*e.g.* Fig. 2-44a) corpus bursae with 3 signa (e.g. Fig. 2-75)...**9**

9.

Forewing postmedial band forming straight line or nearly so (Fig. 2-6); forewing underside with distinct pink flush; hindwing pink, never orange, yellow-orange or yellow...***G. phyllira*** (in part)

Forewing postmedial band distinctly angled at medial vein (Fig. 2-10); forewing underside lacking pink flush; hindwing colour variable, usually orange-pink...***G. parthenice***

10.

Forewing postmedial band reduced (not extending to postcubital stripe) or absent; forewing usually with well-defined transverse pale bar at distal end of cell and / or middle of cell (Fig. 2-12, 2-14), representing traces of postmedial and medial bands; males with fuscous grey hindwing, markings obscure; eyes reduced and adjacent gena exposed; arctic / alpine only...**11**

Forewing postmedial band well developed, extending from costa to postcubital stripe (Fig. 2-8, 2-9, 2-36); males with hindwing markings sharply defined (Figs. 2-8, 2-9, 2-36); eye size variable; not occurring in arctic/alpine habitats...**12**

11.

Antennal scales predominantly pale; forewing length usually less than 14 mm; male vesica shorter than aedeagus; circumpolar arctic / alpine distribution...***G. quenseli*** (in part)

Antennal scales entirely or predominantly black; forewing length usually greater than 14 mm; male vesica longer than aedeagus; southcentral Siberia only...***G. kodara***

12.

Occurring only west of the Great Plains, and with at least one of the following characters: *a)* forewing antemedial band present (Fig. 2-36, 2-37), *b)* medial band extending through postcubital stripe (Fig. 2-36, 2-37, 2-39), *c)* eyes reduced (< 0.70 mm diameter)...**13**

Occurring only east of the Great Plains and / or the Boreal Forest region; forewing antemedial band absent; medial band, if present, usually restricted to cell, not extending through postcubital stripe; eyes not reduced (> 0.70 mm diameter)...**16**

13.

Eyes reduced (< 0.70 mm diameter); male antennal branch length averaging less than 3x segment length; forewing length less than 17mm; Pacific coast from California to British Columbia...**14**

Eyes not reduced (> 0.70 mm diameter); male antennal branch length averaging greater than 3x segment length; forewing length greater than 17 mm; Pacific coast to Rocky Mountain region...**15**

14.

Antennal scales predominantly pale; forewing shape relatively narrow and pointed (Fig. 2-39); antemedial band variable; male hindwing markings discrete; known only from San Francisco Bay area of California...***G. edwardsii***

Antennal scales predominantly or entirely dark; forewing shape relatively broad (Fig. 2-38); forewing antemedial band usually absent; male hindwing markings confluent; coastal British Columbia and Washington...***G. complicata***

15.

Forewing basal band well-developed and hindwing markings never confluent (Fig. 2-37); valve apex broad, rounded (Fig. 2-71a); base of uncus with round, flattened lobes (Fig. 2-2a, 2-71a); southern California only...***G. hewletti*** (in part)

Forewing basal band usually absent; hindwing markings often confluent (Fig. 2-36a,b); valve apex curved or gradually tapering; base of uncus lacking round, flattened lobes (Fig. 2-69a)...***G. ornata*** (in part)

16.

Forewing with at least one of the following: *a)* postmedial band absent or incomplete; *b)* medial band absent; *c)* medial vein line wider than anal vein line...***G. virguncula*** (in part)

Forewing with postmedial band complete; medial band usually present as bar in discal cell; medial vein line variable (Fig. 2-8, 2-9)...17

17.

Hindwing orange or pinkish (very rarely yellow) and markings discrete; no dark scaling along hindwing anal margin; medial vein line wider than anal vein line (fig. 2-8)...***G. virgo***

Hindwing yellow or entirely black, never orange or pink; hindwing markings confluent, usually with extensive dark scaling along anal margin; medial vein line not wider than anal vein line (fig. 2-9)...***G. anna***

18.

Patagia and vertex of head entirely pale-coloured; last two abdominal segments entirely black dorsally, dorsal medial line not expanding near apex of abdomen, or absent entirely; basal portion of cubital vein always pale, often bordered by black scales; midline of ventral abdomen pale without dark spots, or black entirely (females); male aedeagus with row of apical cornuti...***Notarctia***[1]

Patagia and vertex of head usually striped dark and pale, very rarely entirely pale; last two abdominal segments pale or pink laterally, or if dark, then medial abdominal markings expanded; basal portion of cubital vein variable; midline of ventral abdomen with two rows of dark spots, or black entirely; apex of male aedeagus unarmed...**19**

19.

Forewing with **two or more** of the following characters: antemedial band extending to postcubital or beyond; basal band present; medial band extending beyond postcubital stripe; costal portion of postmedial band curved basad; vein lines present on basal half of wing...**20**

Forewing with **no more than one** of the following characters: antemedial band extending to postcubital or beyond; basal band present; medial band extending beyond postcubital stripe; costal portion of postmedial band curved basad; vein lines present on basal half of wing...**35**

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[1] *Notarctia* species are often confused with *Grammia nevandensis* and *G. incorupta*, and are therefore included in this key.

20.

Forewing postmedial band not curved basad near costa, or only slightly so, meeting costa at acute angle; base of anal vein pale-lined (Fig. 2-32, 2-33); forewing length not exceeding 15mm...**21**

Forewing postmedial band curving basad near costa, and/or meeting costa at right angle (*e.g.* Figs. 2-19, 2-20, 2-21, 2-36); base of anal vein variable in colour; forewing length variable, usually > 15 mm...**22**

21.

Antenna predominantly pale-scaled; male antennal pectinations greater than 3x length of segments; hindwing yellow, varying to orange; apical vesica chamber equal in size to medial chamber; Great Plains...***G. blakei***

Antenna with few or no pale scales; male antennal pectinations less than 2.5x length of segments; hindwing greyish-white; apical vesica chamber larger than medial chamber; alpine zone of Colorado Rocky Mountains...***G. cervinoides***

22.

Forewing antemedial band wider than medial band (Fig. 2-24); vein lines absent, except occasionally at base of anal vein (Fig. 2-24b); thorax entirely dark; hindwing antemedial spots absent, medial spot reduced or absent...***G. behrii***

Forewing antemedial band equal to or narrower than medial band, or if wider than medial, only slightly so and with traces of vein lines and / or hindwing antemedial spots; thorax dark or striped, medial spot present or absent...**23**

23.

Forewing basal band and antemedial band absent entirely, or reduced to costal wedge (Figs. 2-34, 2-30)...**24**

Forewing basal and/or antemedial band present, ranging from well-defined band to incomplete line, but not usually reduced to costal wedge (e.g. Figs. 2-21, 2-22)...**25**

24.

Male antennal pectinations less than 3x length of segments; eyes not strongly reduced; base of anal vein and cubital usually pale (Fig 2-34); subalpine habitats of Pacific Northwest and northern Rocky Mountains...***G. elongata***

Male antennae with pectinations greater than 3x length of segments; eyes reduced; base of anal vein and cubital not pale; central Arizona...***G. yavapai***

25.

Forewing AM band usually incomplete (Fig. 2-26, 2-35b) or absent (Fig 2-35a), and never reaching anal margin, and never as well-developed as basal band...**26**

Forewing AM band complete or incomplete, but usually present below postcubital stripe to anal margin (*e.g.* figs. 2-19, 2-22a,b,c, 2-37) usually as well-developed as basal band or more so (*e.g.* Figs. 2-19, 2-21...**27**

26.

Antenna pale-scaled, male pectinations less than 2.5x segment length; forewing elongate, produced apically, and hindwing markings discrete (Fig. 2-35); thorax striped; eyes reduced; alpine zone of Sierra Nevada, California...***G. fergusoni***

Antenna dark-scaled, male pectinations greater than 2.5x segment length; forewing short and broad, hindwing markings confluent (Fig. 2-26); thorax often entirely dark brown; eyes not reduced; eastern Utah to western Colorado...***G. bowmani***

27.

Forewing bands with distinct yellow colour; hindwing ground colour orange-red, marginal markings confluent into broad band (Fig. 2-20); southern AZ to central Mexico at upper elevations...***G. allectans***

Forewing bands wide or narrow, white-tan in colour; hindwing ground colour variable; marginal markings discrete or confluent, but not usually forming broad, solid marginal band (Figs. 2-226, 2-36); western North America...**28**

28.

Hindwing ground colour shades of orange or yellow, without pink; usually with at least traces of pale forewing vein lines; overall relatively large and broad-winged, forewing length usually greater than 18 mm (Fig. 2-36, 2-37)...**29**

Hindwing ground colour with pink, including whitish- or orange-pink; never with forewing vein lines; moderate size, forewing length usually less than 18 mm (e.g. Fig. 2-19, 2-20, 2-21, 2-26)...**31**

29.

Eyes reduced, < 0.65 mm diameter; male antennal pectinations short, 2.4 – 2.8x segment length; antemedial band fragmentary (Fig. 2-25)...***G. eureka***

Eyes not reduced, > 0.65 mm diameter; male antennal pectinations long, usually 3x segment length or more; antemedial band usually well-developed (Figs. 2-36, 2-37)...**30**

30.

Forewing basal band well-developed and hindwing markings never confluent (Fig. 2-37); valve apex broad, rounded (Fig. 2-71a); base of uncus with round, flattened lobes (Fig. 2-71a); southern California only...***G. hewletti*** (in part)

Forewing basal band usually absent; hindwing markings often confluent (Fig. 2-36a,b); valve apex curved or gradually tapering; base of uncus lacking round, flattened lobes (Fig. 2-69a)...***G. ornata*** (in part)

31.

Male antennal pectinations 3.3x segment length or shorter; thorax always striped; hindwing dull yellow-pink; eyes slightly reduced (~ 0.06 mm diameter); Yukon...***G. yukona***

Male antennal pectinations 3.5x segment length or longer; thorax striped or brown / black; hindwing colour variable; eyes normally developed (0.75-1.0 mm diameter); central BC and AB southward...**32**

32.

Male antennal pectinations very long, at least 4.1 to 4.7x segment length, **and** forewing length less than 17 mm; anal vein usually pale-lined at base (Fig. 2-21a); southern California and Channel Islands...***G. ursina***

Male antennal pectinations usually 3.4 to 4x segment length, but if longer, then forewing length greater than 17 mm; anal vein usually not pale-lined at base (Fig. 2-21a); widespread western distribution...**33**

33.

Forewing bands relatively broad and smooth-bordered; thorax almost always striped; subterminal markings of hindwing not extending beyond upper half of margin; several seasonal flights; southeast California to southwest Kansas, south into Mexico...***G. incorrupta***

Forewing bands relatively narrow and of uneven thickness; thorax striped (Great Plains) or black (Great Basin); subterminal markings of hindwing usually extending to near anal margin; one flight annually; Great Plains westward, south to Colorado and Utah...**34**

34.

Hindwing vivid pink; postmedial and subterminal spots reduced, medial spots absent (Fig. 2-27); thorax dark brown; Bryce Canyon region of Utah...***G. brillians***

Hindwing washed-out whitish pink (males) with reduced markings (Fig. 2-22a), or pink to orange-pink with well-developed markings, including medial spots (Fig. 2-22c,d); thorax striped or dark; widespread in western North America...***G. nevadensis***

35.

Forewing lacking pale bands; pale marks entirely absent or reduced to one or two spots in forewing cell (Fig. 2-7b)...**36**

Forewing with pale bands...**37**

36.

Forewing underside with distinct pink flush; forewing length >16 mm; eastern USA from New Jersey to Florida...***G. placentia* (female)**

Forewing underside lacking pink flush; forewing length <16 mm; Colorado to Texas and Utah...***G. f-pallida* (female)**

37.

Hindwing pink, lacking antemedial and medial spots (Figs. 2-6a, 2-7a); FW underside with distinct pink flush...**38**

Hindwing pink, yellow, or orange; forewing underside similar to dorsal surface, or with yellowish basal flush, but lacking pink flush...**39**

38.

Distance from medial to postmedial band at forewing costa equal to or greater than distance from medial to wing base (Fig. 2-7a); New Jersey to Florida...***G. placentia* (males)**

Distance from medial to postmedial band at forewing costa less than distance from medial to wing base (Fig. 2-6a); Great Plains eastward...***G. phyllira*** (in part)

39.

Forewing subterminal band absent or incomplete (Fig. 2-17a,c, 2-18a,b); ventral abdomen usually entirely black...**40**

Forewing subterminal band well-developed (*e.g.* Fig. 2-16, 2-17b); ventral abdomen pale with dark markings...**41**

40.

Forewing length less than 15 mm (mean = 14 mm); Colorado and southeast Utah to Texas...***G. f-pallida* (males)**

Forewing length usually greater than 15 mm (mean 16 mm); southern Ontario and New England south to Georgia and west to Colorado and Texas...***G. figurata* (in part)**

41.

Forewing medial band meeting costa at a right angle or nearly so, such that costal distance between medial band and wing base is only slightly more than distance between medial and postmedial (Figs. 2-15, 2-16, 2-17b,c)...**42**

Forewing medial band meeting costa at acute angle, such that costal distance between medial band and wing base is twice the distance between medial and postmedial, or nearly so (Figs. 2-28, 2-29, 2-31)...**44**

42.

Eyes reduced (< 0.65 mm diameter); male antennal branches short, averaging less than 3x segment length; alpine elevations, California...***G. bolanderi***

Eyes normally developed (> 0.65 mm diameter); male antennal branches long, averaging 3x segment length or more; boreal region and Great Plains west to Sierra Nevada crest of California...**43**

43.

Forewing antemedial band highly reduced or absent; male hindwing with streaked medial and anal margin markings (Fig. 2-28a,b,c) (except some central Utah populations, ssp. *tooele*); hindwing dull pinkish, orange or yellow, rarely bright pink; widespread and common at most elevations throughout western and boreal North America...***G. williamsii***

Forewing antemedial band well-developed, often extending through postcubital stripe (Fig. 2-29); male hindwing markings restricted to postmedial and subterminal markings; hindwing bright pink; restricted to sandy prairie of central Great Plains...***G. favorita***

44.

Forewing length usually greater than 15 mm; male antennal branch length usually greater than or equal to 3x segment length; forewing shape relatively broad and rounded (fig. 2-17b)...***G. figurata*** (in part)

Forewing length usually less than 15 mm; male antennal branch length less than 3x segment length (averaging 2.6 x longer); forewing shape more elongate and pointed apically (Fig. 2-15, 2-16)...**45**

45.

Eyes reduced (< 0.65 mm), diurnal only and not attracted to lights; hindwing markings usually obscure (Fig. 2-15) or entirely greyish; forewing length usually less than 14 mm; grassland habitats of the Great Plains and westward...***G. margo***

Eyes normally developed, greater than 0.70 mm in diameter; nocturnal; hindwing markings well-defined (Fig. 2-16) or hindwing entirely black; forewing length usually greater than 14 mm; Great Lakes region eastward...***G. franconia***

HOLARCTIA M.E. SMITH, REVISED STATUS

Holarctia M.E. Smith 1938b: 6. Type species: *Callarctia turbans* (Christoph, 1982) [junior subjective synonym of *Arctia obliterata* Stretch, 1885], by original designation.

Palearctia Ferguson 1984: 454. **New Synonomy.** Type species: *Arctia glaphyra mannii* Alpheraky 1882, by original designation.

Although *Arctia obliterata* Stretch has invariably been treated as congeneric with *Grammia*, Smith (1938) recognized that it was very divergent morphologically from all other *Grammia* species, despite superficial similarity in wing markings (particularly to *G. virguncula*, Chapter 2). This led her to propose a new subgenus for *G. obliterata*, i.e. *Holarctia* M.E. Smith. Smith did not examine Palaearctic genera now known to be closely related to *Grammia*, but it is now clear that *G. obliterata* exhibits most of the characters considered to be diagnostic for *Palearctia* by Ferguson (1984), and that it does not belong in *Grammia*. This was unfortunately overlooked by Ferguson (1984) when he described the *Palearctia*. Characters that *G. obliterata* shares with, and diagnostic for *Palearctia*, as defined by Ferguson (1984), include the highly reduced apical flat portion of the male valve (Ferguson 1984: 454, figs. 12,13,14) (prominent and lobate or spatulate in *Grammia*), base of the valve costa produced inwardly (Ferguson 1984: 454, figs. 12,13,14) (absent in *Grammia*), apical chamber of vesica equal to or smaller than median chamber (Ferguson 1984: figs. 12a,13a,14a) (large and kidney-shaped in *Grammia*), apex of aedeagus spinulate (Ferguson 1984: 454, figs. 12a,13a,14a) (unmodified in *Grammia*), ductus bursae of female lacking well-defined sclerotized apical collar (Ferguson 1984: 454, fig. 16) (present in *Grammia*), corpus bursae with three signa (Ferguson 1984: 454, fig. 16) (four in *Grammia*). The forewing pattern of *H. obliterata* is very similar to that of the type species of *Palearctia*, i.e.*H. glaphyra manni* (Alpheraky), with four transverse bands or costal marks, and incomplete pale-lined veins.

The large genetic divergence of *obliterata* compared to all other *Grammia* species (Chapter 2), and non-monophyly of *Grammia sensu lato* (Figs. 4-4, 4-5, 4-6) also support placement of *obliterata* in the genus *Palearctia*. Ferguson (1984, 1985) considered

Palearctia to be restricted to the Palaearctic region, but *obliterata* is Holarctic, although the Beringian/northwest North American distribution is indicative of a Palaearctic origin. The reduced eyes of *Palearctia* species are associated with diurnality (Ferguson 1984, 1985), a trait displayed by Yukon populations of *H. obliterata* (G. Anweiler, pers. comm.), but not by the more southerly populations (BCS, unpubl. data).

The placement of *obliterata* in *Palearctia* renders the latter a junior subjective synonym of *Holarctia* M.E. Smith 1938. This is unfortunate since *Holarctia* Smith and *Holoarctia* Ferguson not only have a confusingly similar orthography, but also because members of these genera are superficially similar. Ferguson remarked: "I am aware that the spelling of *Holoarctia* is similar to that of *Holarctia* M.E. Smith, a synonym of *Grammia* Rambur (Arctiidae), and *Holarctias* Prout, a synonym of *Scopula* Schrank (Geometridae), and that it disregards a recommendation of the Code that names with small differences of spelling be avoided. However, it is not a homonym." Although it may be tempting to reverse the precedence of *Holarctia* Smith in favour of *Palearctia* Ferguson since *Holarctia* has not been in general usage while *Palearctia* has, the requirements for maintaining prevailing usage under the provisions of articles 23.9.1.1 and 23.9.1.2 (ICZN 1999) are not met. *Holarctia* M.E. Smith is therefore revised as a senior subjective synonym of *Palearctia* Ferguson.

HOLARCTIA OBLITERATA (STRETCH) REVISED STATUS

FIGS. 2-3, 2-42, 2-74, 2-96.

Arctia obliterata Stretch, 1885: 105.
Arctia turbans Christoph, 1892: 460.
Apantesis turbans (Christoph); Franclemont 1983: 117.
Grammia obliterata (Stretch); Ferguson and Opler 2006: 9.

Type Material

Arctia obliterata: Holotype male [CAS] illustrated in Ferguson (1991) [photograph examined]; the type locality is not stated, and presumed to be western North America.

Arctia turbans: male holotype in ZIN according to Ferguson (1991) [not examined]; the type locality is the "Tunga-Alpen, süd-westlich von Irkutsk".

Diagnosis

Likely to be confused only with *Grammia virguncula* in North America, from which it can usually be distinguished by the presence of two or more pale bars in the costal and/or discal area of the forewing, which are very rare in *virguncula*. The forewing anal and Cu1 lines never extend to the wing margin in *obliterata*, nearly always in *virguncula*. Genitalic differences are discussed under *Holarctia*.

Description

Head - Palps black, frons and vertex pale to yellowish buff, vertex rarely black centrally; male antennae moderately bipectinate, pectinations averaging 5.55×10^{-1} mm, ($n = 6$); female antennae moderately biserrate; dorsal scales dark brown to black; eyes well-developed, slightly reduced with partially exposed gena in Yukon specimens. ***Thorax*** - Vestiture black with pale to yellowish buff borders on vertex, patagia and tegulae; black to yellowish buff ventrally, legs predominantly pale buff, ringed with black at base of segments, giving striped appearance. ***Abdomen*** - Dorsal ground colour dull yellow, pale buff near apex; medial and lateral markings black; medial spots often expanded laterally, sometimes confluent with lateral spots such that ventrum is entirely black with yellow segment margins; pale yellowish buff ventrally, lateral black markings varying from discrete oblong spots to entirely confluent with only distal margins of segments pale. ***Forewing*** - Male forewing length averaging 14.8 mm ($n = 6$ males); black dorsally, vein lines nearly complete, rarely extending through apical area; anal vein line rarely extending beyond halfway to anal angle; lines and bands yellowish buff to pale whitish buff; cubital vein line slightly broader than other vein lines; antemedial, medial and postmedial bands reduced to costal/discal bars or absent, never extending beyond cubital vein (postmedial very rarely so, as fine line); subterminal band complete; ventral markings similar, but dark markings with a paler yellowish cast and pale markings slightly more diffuse; sexes similar. Hindwing - Ground colour deep, dull yellow, rarely varying to orange; black markings variable in extent, but antemedial elements usually lacking, medial spot prominent; postmedial spots well developed, varying from discrete to partially or entirely confluent with irregular subterminal band; ventral markings similar, but dark markings with a paler yellowish cast; sexes similar. ***Male genitalia*** - Distal portion of valve highly reduced, such that the pronounced, pointed saccular extension appears as valve apex; saccular process pronounced; uncus broad-based, process evenly tapered to rounded apex; juxta twice as long as wide, dorsal margin sinuate, convex medially; aedeagus with slight dorsad curve at ⅔ distance beyond base; vesica highly reduced in length and width; basal and medial chamber only slightly wider than width of aedeagus; basal chamber scobinate and slightly sclerotized laterally; distal chamber only slightly larger than medial chamber, very faintly scobinate. ***Female genitalia*** - Ostium bursae with sclerotized collar; ductus bursae short, corpus bursae arising very near ostium; corpus bursae globose to teardrop-shaped, 2 to 3x width of ostium; three scobinate signa, signum one larger than two and three; appendix bursae coiled, evenly tapered; posterior apophysis twice length of papillae anales.

Biology

In North America, *Holoarctia obliterata* inhabits grasslands in dry montane habitats and the northern prairies. It prefers habitats with sparse vegetation cover, such as sandy substrates, eroding slopes, and gravel outwashes. Most adult collection dates range from mid July to mid August, and in the northern parts of its range, *obliterata* often flies with *Grammia nevadensis*. Both sexes come to light, although females rarely so. In the Yukon (and likely Alaska), *obliterata* is diurnal, and males have a rapid, buzzing flight (G. Anweiler, pers. comm.).

Distribution

Holarctic in distribution. In North America, occurs from Alaska and southern Yukon, and primarily east of the Continental Divide from northern B.C. to northern

Colorado and Utah (Ferguson *et al.* 2000), east to Manitoba (Fig. 2-96). The record for Great Bear Lake, NT in Ferguson (1991) is based on abberant specimen of *Grammia virguncula.* In the Palaearctic region, *obliterata* occurs from Russia (Khakassia, East Sayan, Baikal region, Transbaikalia, Amurland, Yakutia) to Mongolia (Murzin 2003).

Molecular Variation

Three specimens of *obliterata* from two sites (Alberta) exhibited three haplotypes, at least 5.33% divergent from all *Grammia* haplotypes, with a maximum intraspecific divergence of 0.15% (Table 2-2).

Remarks

The specimen illustrated as a female *Holarctia (=Palearctia) obliterata* by Murzin (2003: 214) is not *H. obliterata*, and appears to be another species of *Holarctia* or *Sibirarctia* Dubatolov.

GENUS *GRAMMIA* RAMBUR

Grammia Rambur, 1866: 261. Type species: *Bombyx quenseli* Paykull.
Orodemnias Wallengren, 1885: 315. Type species: *Bombyx quenseli* Paykull.
Mimarctia Neumögen and Dyar, 1894: 9. Type species: *Phalaena arge* Drury.

Description

Head - Male antennae bipectinate, pectinations simple to slightly clavate, 1.5x to 5x longer than segment length (Fig. 2-1b); female antennae slightly biserrate to slightly bipectinate (Fig. 2-1b); dorsal antennal scales black, dark brown or pale buff; eyes range from strongly reduced and ellipsoid to well-developed and hemispherical (Fig. 2-1a); vestiture of palpi, frons and vertex ranging from entirely dark brown to black, pale buff, or buff and brown/black. ***Thorax*** - Vertex of thorax, patagia and tegulae usually brown/black centrally, bordered with with pale to yellowish buff, occasionally entirely brown/black; thorax brown/black ventrally, often with pale central tuft at base of coxae, sometimes brown/black; legs variably pale buff, black or combinations thereof. ***Forewing*** - forewings usually with complete set of transverse bands, consisting of basal, antemedial, medial, postmedial and subterminal elements (Fig. 2-1c); longitudinal elements cosisting of pale vein lines, postcubital (Fig. 2-1c) and costal band (Fig. 2-3, 4); ground colour chocolate brown to black, pale markings buff-white to yellowish or pink-buff. ***Hindwing*** - Usually with antemedial, medial, postmedial and subterminal elements (Fig. 2-1c); ground colour highly variable, ranging from pinkish white to orange, yellow, pink, black or variations thereof; markings dark brown to black. ***Abdomen*** - Abdomen with longitudinal series of lateral and dorsal dark spots, sometimes confluent into bands, rarely entirely dark; ventrally with two rows of medial spots, sometimes confluent, or ventrum brown/black entirely; coremata highly reduced, represented by a pair of setose patches between abdominal sternites 7 and 8; corematal setae sparse, short, translucent and deciduous. ***Male genitalia*** (Fig. 2-2a,b) - male valve consisting of simple valve and sacculus; distal portion of valve slightly concave, apex broadly rounded, spatulate, or crescentic; apex often with minute setae; distal region of sacculus forming poorly defined to well-developed medial saccular process; saccular process developed as poorly-differentiated broad, rounded flange; saccular extension ranging from short, broad and triangular to obsolete; uncus simple, gradually taperring to apex, straight in lateral view, or slightly curved ventrally at apex; base of uncus with flat, rounded lobes in one species (*G. hewletti*, Fig. 2-2a); juxta as wide or wider than long, ventral margin convex or slightly cleft, dorsal margin concave and u- to v-shaped; aedeagus three to six times longer than wide, cylindrical to slightly compressed laterally, distal end curving dorsad beyond middle, opening directed right laterad to dorsolaterad; aedeagus lacking cornuti and spinules; vesica approximately equal in length to aedeagus, produced right laterad and dorsad, often curving cephalad; vesica here defined as three-chambered with four variably developed diverticuli (Fig. 2-2b); distal chamber scobinate with short stout spinules; medial chamber unarmed to finely scobinate; spermatophore α-shaped. ***Female genitalia*** (Fig. 2-2c) - antevaginal pouch simple concave pocket; ductus bursae unsclerotized with two sclerotized lateral plates near ostium in subgenus *Grammia* (completely unsclerotized in subgenus *Mimarctia*); corpus bursae pear-shaped to globose, with four rounded signa, consisting of concentric rings of small stout cornuti; appendix bursae coiled approximately 1.25 revolutions.

SUBGENUS *MIMARCTIA* NEUMÖGEN AND DYAR

Diagnosis

Two species are included in the subgenus *Mimarctia*, *Grammia arge* and *G. doris*. Although the wing pattern is superficially much like other *Grammia*, the forewing costal cell is entirely pale-scaled (except sometimes at extreme base), and the costal portion of the postmedial band is angled sharply basad, forming a straight or nearly straight line with the anal portion of the subterminal band (Figs. 2-4 & 2-5). Structurally, the dorsal margin of the male juxta is deeply cleft, v-shaped to slightly u-shaped, with a medial groove extending ventrally; the diverticuli of the male vesica are much larger and more elongate than in any other *Grammia* species (Figs. 2-40b & 2-41b). The female ductus bursae lacks the sclerotized lateral plates (Figs. 2-72 & 2-73). The cremaster of the pupa is elongate, with well-developed longitudinal folds not extending onto distal portion of cremaster (Smith 1938a). The larvae have a complete or partial subdorsal stripe, and the tubercles are dull with finely-barbed setae (Smith 1938a).

GRAMMIA ARGE (DRURY)

FIGS. 2-4, 2-40, 2-72, 2-97.

Phalaena arge Drury, 1773: 35, pl. 18, f. 3.
Bombyx dione Fabricius, 1775: 572.
Noctua incarnatorubra Göze, 1781: 241.
Apantesis nervosa Neumögen and Dyar, 1893: 142.
Arctia arge var. *strigosa* Stretch, 1906: pl. 8 f. 20.
Apantesis arge (Drury); Franclemont 1983: 117.
Grammia arge (Drury); Ferguson and Opler 2006: 10.

Type Material

Phalaena arge: based on a female holotype from New York [lost].

Bombyx dione: described based on an unknown number of specimens [lost?].

Noctua incarnatorubra: described based on an unknown number of specimens; location of type material unknown.

Apantesis nervosa: male holotype in USNM according to Smith (1938a) [not examined].

Arctia arge var. *strigosa*: secondary homonym of *Bombyx strigosa* Fabricius 1793, a subjective junior synonym of *Grammia quenseli* Rambur.

Diagnosis

The lined forewings and broad pale band filling the costal cell distinguishes *G. arge* from all other *Grammia*. Internally, the vesica of the aedeagus exhibits distinctly larger basal diverticula compared to members of the subgenus *Grammia*. See diagnosis under *G. doris* for comparison to that species.

Description

Head - Palps black, frons and vertex pale- to pinkish-buff; male antennae moderately bipectinate, pectinations averaging 2.86 x 10^{-1} mm, (n = 6); female antennae slightly biserrate; dorsal scales predominantly pale buff, black towards apex; eyes well-developed. ***Thorax*** - Vestiture black with wide, pale-buff borders on vertex, patagia and tegulae; sides of ventral thorax black, pale buff to light pinkish buff centrally at base of coxae; coxa and femur reddish pink, ringed with black apically and basally; tibia and tarsi pale buff and black. ***Abdomen*** - Dorsal ground pale pink-buff, apex paler; medial and lateral markings black; medial band thin; pale whitish buff ventrally, lateral black markings reduced, sometimes absent. ***Forewing*** - Male forewing length averaging 18.3 mm (n = 6), females noticeably larger, averaging 23.8 mm (n = 5); black dorsally, vein lines complete, cubital vein line expanded into band; lines and bands whitish buff, rarely with pinkish cast; antemedial and medial band usually expressed only as broad triangular mark in discal cell, rarely absent; postmedial band broad, rarely reduced and/or fragmented; postmedial very strongly angled at M_3, such that postmedial and subterminal band form an 'X'; subterminal and postcubital well developed; costal cell nearly always entirely pale; fringe and anal margin concolourous with pale markings, anal margin band broad, often confluent with anal vein line; ventral markings similar, but dark markings slightly paler, and distinct pinkish red marginal outline; sexes similar, although females significantly larger as noted above. Hindwing - Ground colour pale pinkish white, females slightly pinker; black markings highly reduced or absent; variable in extent; antemedial spots when present not streaked basad, more clearly expressed ventrally; medial spot small but distinct and crescentic; postmedial and subterminal elements reduced or absent, fragmented by pale vein lines; ventral markings and colours similar to dorsum, but with distinct pinkish red marginal terminal line; sexes similar. ***Male genitalia*** - Distal portion of valve gradually tapered, caudoventral margin slightly concave, apex rounded; saccular extension poorly to moderately developed, saccular process moderately developed; juxta slightly longer than wide, with u-shaped dorsal cleft extending halfway to base; pronounced medial dorsoventral groove; uncus broad-based, process evenly tapered to point, 3-4x as long as width of base; aedeagus relatively short and wide, curved dorsad at apex; vesica extending right laterad; basal chamber and diverticulum reduced; medial diverticulae enlarged and prominent, particularly 1st medial; distal chamber large and irregular in shape, scobinate; vesica approximately twice as long as aedeagus. ***Female genitalia*** - Ductus bursae unsclerotized, lacking lateral plate near ostium; corpus bursae oblong, 4-5x width of ostium bursa; four moderately sized, rounded signa; signa coarsely scobinate; appendix bursae evenly coiled; posterior apophysis slightly longer than papillae anales.

Biology

This species is multivoltine throughout most, if not all, of its range. It occurs in May and August in southern Ontario, and March through October in the southeastern United States. *Grammia arge* is often a common species of dry woodlands, meadows, pastures and grasslands. Both sexes come to light.

Distribution

Occurs from Ontario, Quebec and New England south to Florida, west to Colorado (Ferguson *et al.* 2000) and North Dakota; occurs south into Mexico, and Smith

(1938a) reports a single record for Guatemala City, Guatemala.

Molecular Variation

Sequences for fourteen specimens of *G. arge* were available, representing four populations (ON [2], NC, PA). The five haploptypes were monophyletic, and exhibited low divergence (Table 2-2, Fig. 2-132). *Grammia arge* haplotypes were most similar to those of *G. doris*, with a minimum interspecific difference of 4.9% (Table 2- 1b).

GRAMMIA DORIS (BOISDUVAL)

FIGS. 2-5, 2-41, 2-73, 2-98.

Chelonia doris Boisduval, 1869: 77.
Chelonia nerea Boisduval, 1869: 77.
Arctia michabo Grote, 1875: 196.
Arctia minea Slosson, 1892: 257.
Apantesis doris (Boisduval); Franclemont 1983: 117.
Apantesis doris minea (Slosson); Franclemont 1983: 117.
Grammia doris (Boisduval); Ferguson and Opler 2006: 10.
Grammia doris minea (Slosson); Ferguson and Opler 2006: 10.

Type Material

Chelonia doris: described from an unstated number of specimens, with a female syntype in the Oberthür Collection according to Smith (1938a). The types of the North American taxa described by Boisduval in the Oberthür Collection should be in the USNM (with the remaining Oberthür specimens in the BMNH), according to Miller and Brown (1981) [not examined]. The type locality was given as "from the South" [southern California, USA], but *doris* is not known to occur in California, nor anywhere south of British Columbia or west of Colorado and Texas. Other taxa described by Boisduval (1869) are all Californian, so this offers no clues as to where the *G. doris* types really originated. Nearly all North

American taxa described by Boisduval between 1852 and 1872 originated from California and Mexico, and it is possible that the *G. doris* types originated from the latter, since it occurrs in central Texas. Because of the geographic variablity in *G. doris*, and the distinct possiblity that two species are currently included under nominal *G. doris*, the **type locality** is hereby restricted to the vicinity of Dallas, Dallas Co., Texas, USA, where *G. doris* is known to occur.

Chelonia nerea: description based on an unstated number of female specimens; as noted above, the type material was part of the Oberthür Collection according to Smith (1938a), and the type should be in the USNM or BMNH [not examined]. For the same reasons discussed above under *Chelonia doris*, the **type locality** of California is likely erroneous, and is hereby restricted to the vicinity of Dallas, Dallas, Co., Texas, USA, where *G. doris* is known to occur.

Arctia michabo: Male holotype in BMNH according to Hampson (1901) and Smith (1938a) [not examined]; female type in BMNH [photograph examined]; the type locality is Nebraska, [USA].

Arctia minea: described from one male and two female syntypes from Franconia, New Hampshire, [USA]; male syntype in USNM according to Smith (1938a) [not examined].

Diagnosis

The lined forewings and broad pale band filling the costal cell distinguishes *G. doris* and *G. arge* from all other *Grammia*. Compared to *G. arge, G. doris* has a narrowly lined Cu vein, not broadly banded as in *G. arge,* and the postmedial band meets the costa at a right or slightly obtuse angle, compared to an acute angle in *G. arge*. The hindwing postmedial and subterminal spots are much larger in *G. doris*, and never 'split' by pale vein lines as in *G. arge* specimens with well-developed spots. Internally, the valve is distinctly narrow and crescentic, unique among *Grammia.*

Description

Head - Palps black, frons and vertex pinkish buff; male antennae moderately bipectinate, pectinations averaging 3.74 x 10^{-1} mm, ($n = 4$); female antennae slightly biserrate; dorsal scales dark brown, rarely with scattered buff scales; eyes well-developed. ***Thorax*** - Vestiture black with pink-buff borders on vertex, patagia and tegulae; sides of ventral thorax black, pinkish centrally at base of coxae; coxa and femur black basally, pinkish red apically; tibia pinkish buff and black or entirely black; tarsi black. ***Abdomen*** - Dorsal ground colour pink, apex rarely slightly paler; medial and lateral markings black; medial band variable, nearly obsolete (southern populations) to broad (boreal populations); pinkish buff ventrally, lateral black markings variable, but not confluent. ***Forewing*** - Male forewing length averaging 19.9 mm (n = 4 males), northern populations averaging slightly smaller; black dorsally, vein lines complete, lines and bands light pinkish buff, rarely bright pink; antemedial and medial band variable, usually restricted to bar in discal cell, sometimes absent; postmedial band usually well-developed, sometimes reduced and fragmentary or reduced, strongly angled at M_3; subterminal and postcubital well developed; costal cell entirely or mostly pale, except at wing base; fringe and anal margin concolourous with pale markings, anal margin band broad, often conlfuent with anal vein line; ventral markings similar, but dark markings slightly paler, and pale markings with distinct pink cast; sexes similar. Hindwing - Ground colour light pink, black markings variable in extent; antemedial spots when present not streaked basad, more clearly expressed ventrally; medial spot usually large and prominent; postmedial and subterminal elements never confluent, subterminal spots reduced or absent; postmedials usually consisting of three discrete spots; ventral markings and colours similar to dorsum, sexes similar. ***Male genitalia*** - Distal portion of valve narrow and elongate, crescentic with rounded apex; saccular extension moderately developed, appearing prominent as a result of narrow distal portion of valve; saccular process moderately developed; juxta slightly longer than wide, with v-shaped dorsal cleft extending ⅔ of distance to base; pronounced medial dorsoventral groove; uncus broad-based, process evenly tapered to point, 3-4x as long as width of base; aedeagus relatively short and wide, curved dorsad at apex; vesica with basal and medial chamber approximately equal in length and width; basal chamber and diverticulum reduced; medial diverticulae enlarged and prominent, particularly 1st medial; distal chamber medium-sized, twice as long as width of medial chamber, only slightly wider than medial chamber; apical and medial chamber finely scobinate; vesica about twice as long as aedeagus. ***Female genitalia*** - Lateral plates of ostium bursae absent; ductus bursae unsclerotized, relatively short and narrow; corpus bursae of moderate size, approximately 4x width of ostium, globose; signa round, to rounded-triangular, scobinate, and relatively large; posterior apophysis slightly longer than papillae anales.

Biology

Although it can be locally common in the southeastern United States, this is one of the most rarely collected *Grammia* species, and most records represent a few historical specimens. Unlike other rarely collected *Grammia*, its scarcity cannot be attributed to diurnality. Habitat preferences are not clear in the northern parts of the range, since most records are based on single specimens. Extensive trapping in dry, open forest habitats in southern Ontario have not yielded this species (J. Troubridge, pers. comm.), nor has it been recorded in extensive surveys carried out in dry and mesic boreal forest, and prairie grassland habitats in western Canada (C. Schmidt, unpubl. data). The few recent records indicate that this species may be associated with wetlands or riparian habitats.

Distribution

Occurs from Newfoundland west to southern British Columbia, south to Texas and Florida, but records are lacking for many regions (Fig. 2-98).

Molecular Variation

Two specimens from the northwestern (ssp. *minea*) and one from the southeastern (ssp. *doris*) range limits of *doris* exhibited two haplotypes, with 1.3% divergence between the two geographical regions (Table 2-2, Fig. 2-132). *Grammia doris* haplotypes were most similar to *G. arge* (Fig. 2-132), with a minimum difference of 4.9% (Table 2-2).

Remarks

The rarity of this species across most of its range is puzzling, and may be the result of inadequate sampling in the appropriate habitat. Under the current concept of *doris*, this species has an exceptionally large geographic range, occurring from the subtropical region (Florida) northward and nearly reaching the subarctic (Newfoundland). This is very unusual for any non-migratory moth species, certainly so for *Grammia*, and suggests that subspecies *minea* should perhaps be treated as a distinct species. The molecular divergence between northwestern and southeastern populations supports this, but additional samples from intervening regions should be evaluated, both genetically and morphologically. Unfortunately, this species is rarely collected, and the paucity of specimens currently available prevents any further insight into this interesting situation. *Grammia doris* was flagged as a species of special interest in Ohio (Metzler & Lucas, 1990) due to its rarity in that state.

GRAMMIA DORIS DORIS (DRURY)

FIGS. 2-4A, B

Diagnosis

Distinguished from ssp. *minea* by the slightly larger size (mean forewing length = 21 mm), wider forewing bands, and smaller hindwing spots.

Biology

Adult collection dates range from late May to August, indicative of more than one generation; Florida records are primarily for May and August.

Distribution

Southern Texas and Florida northwards; due to the paucity of specimens, the northern extent of ssp. *doris* in relation to ssp. *minea* is unclear.

GRAMMIA DORIS MINEA (SLOSSON)

FIG. 2-2-4C

Diagnosis

Distinguished from nominal *G. doris* by the slightly smaller size (mean forewing length = 19 mm), thinner forewing pale bands, and larger hindwing spots.

Biology

Adult collection dates indicate a single annual generation, with the flight peak between late May and mid June. As discussed under *G. doris*, the habitat preference of *G. d. minea* is not clear, but may include wetlands.

Distribution

Southern British Columbia east to Newfoundland and New Brunswick; due to the paucity of specimens, the southern extent of ssp. *minea*, and relationship to ssp. *doris*, is unclear.

SUBGENUS *GRAMMIA* RAMBUR

Diagnosis

All but two of the 36 species of the genus are included in the subgenus *Grammia*. Although the wing pattern is superficially like *Mimarctia*, the forewing costal cell is never entirely pale-scaled, and the costal portion of the postmedial band is not angled sharply basad. Structurally, the dorsal margin of the male juxta is broadly concave and u-shaped (somewhat v-shaped in *Mimarctia*). The male vesica is moderately developed with poorly to moderately differentiated chambers and diverticuli (Figs. 2-44 – 2-71); *Mimarctia* exhibits large, well defined chambers and diverticuli (Figs. 2-40, 2-41). The male distal portion of valve is well developed, simple, and rounded to slightly pointed (rounded or sickle-shaped in *Mimarctia*). The female ductus bursae has two sclerotized lateral plates near the ostium, absent in *Mimarctia*. Where known, the cremaster of the pupa is short and broad, not elongate as in *Mimarctia*, and lacks the basal folds or grooves (except for *G. virgo*) of *Mimarctia* (Smith 1938a,b). The larval tubercles are shiny silvery-white not dull as in *Mimarctia*, with coarsely-barbed (vs. finely barbed) setae (Smith 1938a).

GRAMMIA PHYLLIRA (DRURY)

FIGS. 2-6, 2-43, 2-75, 2-99.

Bombyx phyllira Drury, 1773: pl. 7 f. 2.

Geometra b-ata Göze, 1781: 428.

Arctia oithona Strecker, 1878: 131.

Arctia rectilinea French, 1879: 45.

Arctia dodgei Butler, 1881: 136.

Arctia rectilinea var. *conspicua* Stretch, 1906: 120, pl. 8 fig. 2.

Apantesis favorita ab. *favoritella* Strand, 1919: 284. **Revised Synonymy.**

Apantesis phyllira (Drury); Franclemont 1983: 117.

Apantesis oithona (Strecker); Franclemont 1983: 117.

Grammia phyllira (Drury); Ferguson and Opler 2006: 11.

Grammia phyllira (=*avoritella* [Strand]); Ferguson and Opler 2006: 11. [misspelling]

Type Material

Bombyx phyllira: described from a female specimen [lost] from New York.

Geometra b-ata: described from an unknown number of specimens; type locality and type material not known.

Arctia oithona: A female syntype [FMNH, photo examined] labelled "Arctia oithona/ Dallas, Tex. Streck./ orig. Type; J. Boll", "30.", "11. V.", "172.", "orig./ type", LECTOTYPE ♀/ det. A. Watson 1966", "Lepidoptera Type/ Photograph No. 196/ Field Museum", C.N.C./ colour slide/ 662209", "LECTOTYPE/ Arctia/ oithona Strecker/ B.C. Schmidt 2007" is hereby designated **lectotype** to stabilize the name. The type locality is Dallas, [Texas, USA].

Arctia rectilinea: described from two male and two female syntypes, presumed lost. The type locality is Carbondale [Illinois?] acc. to Smith (1938a).

Arctia dodgei: based on a female holotype [BMNH, photograph examined]; the holotype bears no locality data, although the original description states that *dodgei* may be a "Mexican representative" of *phyllira*; *phyllira* is not known to occur in Mexico.

Arctia rectilinea var. *conspicua*: types probably lost; type locality not stated; *conspicua* is an unavailable infrasubspecific name, referring to variants with partially developed forewing vein lines.

Apantesis favorita ab. *favoritella*: Strand (1919) based this name on Hampson's (1901: 406) description of *Arctia favorita* "Ab. 1", which he describes as having the "forewing bands absent, except the postmedial and subterminal." (Hampson 1901). Since this form is not known to occur in *G. favorita*, and since Hamspon's concept of *G. phyllira* included not only *G. phyllira (sensu stricto)* but also *G. figurata* and *G. f-pallida*, it is most likely that his "Ab. 1" describes the unlined form of *G. phyllira*; *favoritella* is therefore transferred to the synonymy of *phyllira*.

Diagnosis

The lined form of *G. phyllira* prevalent throughout the Great Plains could only be mistaken for *G. parthenice*, but *G. phyllira* can easily be distinguished by the pinkish cast on the forewing underside (cream in *G. parthenice*), and the straight, not angled postmedial line. The unlined form is similar to *Grammia placentia* and some specimens of *G. figurata*, but *G. figurata* has yellow-buff ventral forewing bands, not pink; *G. placentia* can be distinguished by its entirely dark, not spotted ventral abdomen, larger size, wider space between the medial and postmedial forewing band at the costa, and females which lack forewing bands.

Description

Head - Palps black; frons and vertex pale buff; male antennae strongly bipectinate, pectinations averaging 5.84 x 10^{-1} mm, ($n = 6$); dorsal scales dark brown to black, sometimes with scattered buff scales; eyes well developed, mean diameter 1.07

mm ($n = 6$). ***Thorax*** - Vestiture black with pinkish buff to pale buff borders on vertex, patagia and tegulae; sides of thorax dark brown ventrally, with orange-pink vestiture at base of coxae; legs buff-coloured and dark brown to black dorsally, predominantly black ventrally. ***Abdomen*** - Dorsal ground colour pinkish red, apex often pale buff; medial and lateral markings black; pale to yellowish buff ventrally, lateral black spots not confluent. ***Forewing*** - Male forewing length averaging 16.9 mm ($n = 6$ males); dark brown to black dorsally, vein lines complete, reduced or absent; bands rich creamy buff to pinkish buff; medial, postmedial, subterminal bands and postcubital stripe generally well developed, antemedial reduced to thickened bar at costa or absent entirely; postmedial not angled at M_3; transverse bands not extending beyond postcubital stripe; fringe entirely cream, costa variably cream and dark; anal margin with relatively broad cream line; ventral markings similar, but dark colours slightly paler, and light bands with distinct yellow-pink hue. Hindwing - Ground colour pink to orange-pink; antemedial spots lacking, medial spot absent to well-developed; postmedial spots relatively large, but not confluent with reduced subterminal band; fringe pink and pale buff; ventral dark markings slightly paler but otherwise similar to dorsum. ***Male genitalia*** - Distal portion of valve tapering to pointed, slightly rounded apex; saccular extension moderately developed, saccular process moderately developed; uncus broad-based, process evenly tapered to point, 2x as long as width of base; juxta 1.5 x wider than long, dorsal margin with broad u-shaped concavity; aedeagus with dorsad curve at ⅔ distance beyond base; vesica with basal and medial chamber approximately equal in length and width, not scobinate; distal chamber medium-sized, twice as long as width of medial chamber, kidney-shaped, finely scobinate; vesica as long as or slightly shorter than aedeagus. ***Female genitalia*** - Ductus bursae unsclerotized, slightly narrowed medially; corpus bursae globose, 3x width of ostium bursa; signa round to slightly elliptical, relatively large, coarsely scobinate; coil of appendix bursae elbowed; posterior apophysis 1.5 – 2x longer than papillae anales.

Biology

Adults have been collected from March into October in the southern United States, indicating two or possibly three generations. Bivoltine as far north as South Dakota, Illinois, New York and southern Ontario with flights in May to June and August

– September. Prairie province and central Ontario records indicate one peak flight in mid July. *G. phyllira* occurs in dry, open woodland and grassland. Although common in much of its southern range, this species becomes very localized further north, occuring only in sandy prairie habitats in western Canada.

Distribution

Found from Quebec (Handfield 1999) and New England south to Florida, west to Texas, Colorado and Alberta (Fig. 2-99).

Molecular Variation

Eight specimens of *G. phyllira* from five localities (ON, KY [2], AB, CO) exhibited seven haplotypes (Fig. 2-132, Table 2-2) distinct from other *Grammia* haplotypes by at least 9%. Divergence among *G. phyllira* haplotypes was high, with a maximum of 2.83% (Fig. 2-132, Table 2-2). Although intraspecific variation was high compared to that of other monophyletic *Grammia* species clusters, there was no indication that molecular variation was geographically structured, with highly divergent haplotypes co-occuring in the Ottawa, ON region (PY5 and PY6: Fig. 2-132, Appendix 2-1). Haplotypes did not cluster according to wing phenotype (lined vs. unlined), with PY1 to PY4 haplotypes correspoding to lined forms, and PY5 to PY7 being unlined forms, although all samples of lined forms were most similar to each other (Fig. 2-132).

Remarks

G. oithona was for a time considered specifically distinct from *G. phyllira* (Franclemont 1983), based on the presence of forewing vein lines in *G. oithona* and absence thereof in *G. phyllira*. It is now clear that both forms are present in most populations, with varying frequency. A reared series of specimens from a female of the lined form show specimens varying from unlined to lined and partly lined [Chicago, IL; CNC]. Over 95% of specimens from Great Plains populations (Alberta, Manitoba, Kansas, Oklahoma, northern Texas) are of the lined form, while the unlined form predominates in eastern North America; Ontario and Illinois populations are predominantly unlined or partially lined, while northwestern Georgia populations are slightly more than half unlined (J. Adams, pers. comm.), and lined forms are extremely rare in Florida.

Although it is clear that lined and unlined forms *per se* do not represent two different species since reared F1 siblings exhibit both forms (BCS, unpubl. data), the possibility that two species (both with lined and unlined forms) are currently included under *G. phyllira* should not be ruled out; the Great Plains populations (*oithona*) are on average smaller with a more elongate wing shape, and the divergence in molecular variation between eastern and western populations is larger than the average intraspecific variation within other monophyletic mtDNA *Grammia* lineages. Molecular and phenotypic variation of geographically intermediate populations needs to be evaluated.

GRAMMIA PLACENTIA (J.E. SMITH)

FIGS. 2-7, 2-44, 2-76, 2-100.

Phalaena placentia Smith, 1797: 129, pl. 65.
Arctia flammea Neumögen, 1881a: 9.
Apantesis placentia (Smith); Franclemont 1983: 117.
Grammia placentia (Smith); Ferguson and Opler 2006: 11.

Type Material

Phalaena placentia: described from an unstated number of specimens, although only a female is illustrated; The Smith types are lost; the type locality is Georgia, [USA].

Arctia flammea: described from a female holotype from Indian River, Florida, [USA] [USNM, not examined].

Diagnosis

The wing pattern and colour is similar to *G. phyllira*, but *G. placentia* has broader, larger wings, the last abdominal segment is entirely dark not black and pale, and the roughly triangular area formed by the forewing medial and postmedial band is much wider at the costa, three to four times the distance at the costa than at the postcubital versus approximately two times in *G. phyllira*. Female *G. placentia* resemble those of *G. f-pallida*, but have discrete hindwing spots rather than a broad, even marginal band.

Description

Head - Palps black; frons and vertex creamy buff; male antennae strongly bipectinate, pectinations averaging 7.17×10^{-1} mm, ($n = 5$); female antennae slightly bipectinate; dorsal scales dark brown to black; eyes well developed, mean diameter 1.16 mm ($n = 5$). ***Thorax*** - Vestiture black with creamy buff to pinkish borders on vertex, patagia and tegulae; females usually entirely dark brown - black; enirely dark brown to black ventrally; legs dark brown to black, base of forecoxa bright pink-red in males, entirely dark in females. ***Abdomen*** - Dorsal ground colour deep pinkish red, last segment entirely black; medial and lateral markings black; entirely dark brown to black ventrally in both sexes. ***Forewing*** - Male forewing length averaging 19.6 mm ($n = 5$ males), relatively broad, more so than other *Grammia*; dark brown to black dorsally, vein lines absent; bands creamy buff; medial, postmedial, subterminal bands and postcubital stripe well developed in males; females entirely dark brown or with medial and postmedial reduced to one to two pale bars or dots, rarely with vestigial, broken bands; fringe, anal margin and costa cream; ventral markings similar, but dark colours slightly paler and with an overall pink-red cast. Hindwing - Ground colour deep pinkish red; black markings highly reduced, but medial discal spot prominent; postmedial spots discrete, small; supterminal band thin, or absent entirely; fringe pink and dark brown; ventral dark markings slightly paler and with pinkish cast. ***Male genitalia*** - Distal portion of valve elongate, tapering to rounded apex; saccular extension poorly developed, saccular process reduced; uncus broad-based, process evenly tapered to point, 1.5 × as long as width of base; juxta 1.5 × wider than long, dorsal margin with shallow, broad u-shaped concavity; aedeagus with dorsad curve at ⅔ distance beyond base; vesica with basal and medial chamber approximately equal in length and width, not scobinate; distal chamber large, 3 × longer than width of medial chamber, kidney-shaped, scobinate; vesica slightly longer than aedeagus. ***Female genitalia*** - Ductus bursae unsclerotized, slightly narrowed medially; corpus bursae globose, 3 × width of ostium bursa; signa round to slightly elliptical, relatively large, coarsely scobinate; coil of appendix bursae elbowed; posterior apophysis 1.5 – 2 × longer than papillae anales.

Biology

Adult collection dates range from March to October, with abundance peaks apparent in May and July, indicating at least two annual generations. *Grammia placentia* occurs in dry, sandy open wooded areas, and both sexes come to light.

Molecular Variation

Six specimens from four localities (GA [3], FL) exhibited four haplotypes, with a maximum intraspecific difference of 0.6% (Table 2-2). *Grammia placentia* formed a monophyletic, highly divergent lineage with respect to all other *Grammia*, with a minimum interspecific divergence of 6% (Table 2-2).

Distribution

Grammia placentia has a restricted distribution, and it occurs only in the southeastern United States from South Carolina to Florida, with an isolated record from the New Jersey pine barrens (Fig. 2-100), where it occurs in localized populations (D. Schweitzer, *in litt.*).

GRAMMIA VIRGO (LINNAEUS)

FIGS. 2-8, 2-45, 2-77, 2-101.

Bombyx virgo Linnaeus 1758: 501.
Euprepia virgo var. *citrinaria* Neumögen and Dyar, 1893: 142.
Grammia virgo var. *simplex* Stretch, 1906: pl.5 f.14, pl.8 f.4.
Apantesis virgo (L.); Franclemont 1983: 117.
Grammia virgo (L.); Ferguson and Opler 2006: 10.

Type Material

Bombyx virgo: female lectotype in the Museum Ludovicae Ulricae Reginae, Uppsala, Sweden, designated and illustrated by Mikkola and Honey (1993) [photo examined]; type locality restricted to Philadelphia, Pennsylvania, USA by Mikkola and Honey (1993).

Euprepia virgo var. *citrinaria*: female holotype in USNM, type no. 33683 [not examined]; type locality not stated; *citrinaria* is an unavailable infrasubspecific name, based on the rare yellow-hindwing form.

Grammia virgo var. *simplex*: types probably lost; type locality not stated; *simplex* is an unavailable infrasubspecific name, referring to variants lacking the FW medial transverse band. Although Stretch (1906) does not provide a description of *simplex*, the illustrated specimens are identical to illustrations of *virgo* except that *simplex* lacks the medial band. Stretch (1906) does not indicate *simplex* as being a new name, despite indicating other new names as "n. var.". This may have been an accidental omission on his part, since there are no other sources that indicate the name was published earlier.

Diagnosis

Grammia virgo is the largest member of the genus, although there is some size overlap with *G. parthenice* where the two occur together. *G. virgo* is distinctive, although it is occasionally confused with *G. parthenice*, but the hindwing medial discal spot of *virgo* is absent in *G. parthenice* (very rarely lacking in *G. virgo*). The forewing medial vein line is wider than the anal vein line in *virgo*, both equally thin in *G. parthenice*, and the angle of the 'break' in the postmedial band is more pronounced in *G. virgo* than *G. parthenice*; although there is size overlap between the two species as a whole, *G. virgo* s always larger when specimens from the same geographic region are compared. *Grammia virgo* usually flies 3-4 weeks earlier in the season than *G. parthenice*.

Description

Head - Palps black, frons and vertex yellowish to creamy buff; male antennae moderately bipectinate, pectinations averaging 6.40×10^{-1} mm, ($n = 10$); female antennae slightly bipectinate; dorsal scales dark brown to black with scattered buff scales; eyes well-developed. ***Thorax*** - Vestiture black with yellowish to creamy buff borders on vertex, patagia and tegulae; entirely dark brown to black ventrally, rarely brownish yellow tuft at base of forecoxa; legs entirely or predominantly black, tibia sometimes buff dorsally. ***Abdomen*** - Dorsal ground colour orange to orange-pink, very rarely yellow in yellow-hindwing forms; apex pale buff; medial and lateral markings black; medial band usually narrow, sometimes reduced to series of dots; ventrally usually entirely black, lateral black spots sometimes incompletely conflulent such that a pale medial line is evident, rarely with distal margins of segments pale. ***Forewing*** - Male forewing length averaging 24.2 mm ($n = 6$), averaging smallest for ssp. *borea*, largest for ssp. *gigas*; black dorsally, vein lines complete, lines and bands yellowish buff to creamy buff; cubital band expanded slightly relative to other vein lines, radial vein line sometimes so; antemedial band usually absent entirely, or visible as slight pale bar along costa; postmedial band variable, most often present as rectangular bar across discal cell onto costa, rarely extending slightly beyond cubital vein; postmedial and subterminal bands well developed; postmedial angled strongly at M_3, not extending through postcubital stripe; fringe, costa and anal margin concolourous with pale markings; ventral markings similar, but dark markings slightly paler, and with a distinct yellowish cast overall; sexes similar. Hindwing - Ground colour pink to orange-pink, rarely yellow; black markings moderately variable in extent; antemedial spots consisting of costal, discal and anal spots, discal spot nearly always present and well-developed; postmedial and subterminal spots well developed, not confluent except near tornus; ventral markings similar, but colours more washed-out and with overall yellowish cast; sexes similar. ***Male genitalia*** - Distal portion of valve gradually tapering to rounded or slightly pointed apex; saccular extension poorly to moderately developed, saccular process moderately developed; uncus broad-based, process tapered to point, 2 × as long as width of base; juxta 2-2.5 × wider than long; aedeagus with dorsad curve at ⅔ distance beyond base; vesica with basal and medial chamber approximately equal in length and width, not scobinate; second medial diverticulum elongate, prominent; distal chamber medium-sized, twice as long as width of medial chamber, kidney-shaped, finely scobinate; vesica longer than aedeagus. ***Female genitalia*** - Ductus bursae unsclerotized, narrowed slightly distad of appendix bursa; corpus bursae globose, 4 × width of ostium bursa; signa round to rounded triangular, relatively small, moderately scobinate; coil of appendix bursae evenly rounded; posterior apophysis 1.5 – 2 × longer than papillae anales.

Biology

G. virgo is essentially a species of mesic deciduous and mixed forests, associated with natural forest openings such as wetlands and meadows, and disturbed habitats such as pastures and roadsides. Adults are often common to abundant, and fly in a single yearly generation. In the northern parts of its range, *virgo* flies in July, and September to October in the southeastern US. The flight season peaks about two to three weeks earlier than *G. parthenice*. Both sexes come to light, although females very rarely so.

Distribution

Occurs across the boreal region from northeastern B.C. east to Nova Scotia, and south to Florida. Absent south and west of the northern Great Plains, and west of the Rocky Mountains, occuring as far south as central AB and at least to North Dakota (Fig. 2-101), with a single record from east-central Nebraska (Ferguson *et al.* 2000). There are historical records of a specimen each from Victoria and Vancouver, B.C. [CNC] but these appear to represent accidental introductions since there are no known extant populations west of the Rocky Mountains. There are isolated literature records for Provo, Utah and Durango, Colorado (Smith 1938a), but I have not seen these or other specimens from this region.

Molecular Variation

Twenty-five samples of *Grammia virgo* representative of 12 localities from across the species' range exhibited 14 haplotypes (Table 2-2). All but two of the *G. virgo* haplotypes formed a relatively divergent lineage (minimum between-species divergence of 5.6%), within which there was moderate divergence (Fig. 2-132). One haplotype fell within each of the Kodara and Western lineage, (Fig 2-132, 2-133), both highly divergent from the Virgo lineage, and resulting in unusually high within-species divergence of 7.1%. These haplotypes may represent introgressed mtDNA as a result of hybridization, as discussed in Chapter 3, although additional molecular data should be sought to substantiate the validity of these divergent haplotypes.

Remarks

Grammia virgo exhibits considerable geographic variation, here segregated into two subspecies: the nominal subspecies throughout Canada and most of the eastern U.S., and the extremely large, vividly coloured populations of the southeastern U.S., described as a new subspecies below.

The level of mtDNA divergence within *G. virgo* is consistent with or exceeds that observed between some *Grammia* sister species, in that samples of the southeastern U.S. populations (ssp. *gigas*) showed two haplotypes at least 0.9% divergent from all other *G. virgo* haplotypes. There was no evidence of haplotype sharing between *G. virgo* and other species (although two of 25 haplotypes fell well outside of the *virgo* lineage, see above), and I therefore consider the genotypic variation of *G. virgo* to reflect the genealogy of *virgo* rather than novel introgressed genotypes. Other than the larger size and somewhat brighter colours of specimens from these southern populations, I could find no structural differences among northern and southern specimens. I therefore treat the southeast populations as a subspecies until additional specimens can be examined for both phenotypic and genotypic variation from populations geographically intermediate between the two putative subspecies. The phylogeography of *G. virgo* is suggestive of more than one refugium during the last glacial maximum, with the V12-13 lineage (Fig. 2-132, 2-136) haplotypes restricted to North Carolina and Tennessee. Although the distance analysis showed [V9-VI11 + VI12-VI13] as sister group to VI1-VI8, maximum parsimony resolved [VI10+VI1] as sister to VI13 (ssp. *gigas*) (Fig. 2-136).

GRAMMIA VIRGO VIRGO (LINNAEUS)

FIGS. 2-8A, C.

Diagnosis

The nominal subspecies of *G. virgo* averages slightly smaller, with less intensely-coloured hindwings than ssp. *gigas*, (male forewing length 22.2 mm).

Distribution

The nominate subspecies occurs from the Great Lakes region and Atlantic seaboard south through New England, to at least West Virginia. Boreal populations (Fig. 2-8c) occur west to northeastern B.C.

GRAMMIA VIRGO GIGAS SCHMIDT, NEW SUBSPECIES

FIG. 2-8B.

Type Material

Holotype **-** ♀. Highlands, North Carolina, USA, 17 July 1957. C.J. Durden, coll. [CNC]. ***Paratypes*** **-** 30♂♂ 2♀♀. **USA: North Carolina:** Same data as holotype, 1♂ [CNC]; same locality as holotype, 27 July 1957 (1♂), 26 July 1957 (3♂♂), 25 July 1957 (3♂♂) [CNC]; Highlands, Horse Cove, 3 August 1957, C.J. Durden, 1♂, [CNC]; Highlands, August 1951, E.C. Zimmerman, 1♂, [CNC]. **South Carolina:** McClellanville, 12-21 September 1970, E.G. Munroe, 1♂ [CNC]. **Georgia:** Rabun Co., Glassy Mtn. Tower, 25 July 1964. L. Cambre, coll. 1♂ [BERK]. **Tennessee:** Great Smoky Mtns. National Park, Cades Cove loop road, 25 July 2000. P. Goldstein, coll. ♂ [BERK]. **Kentucky:** Morehead, 5-9 July 1962, Freeman & Lewis, 6♂♂ 2♀♀ [CNC]; 22-28 July 1963, Freeman, 7♂♂ [CNC].

Etymology

The name *gigas* is derived from latin for gigantic, since females of this subspecies are the largest of any *Grammia*.

Diagnosis

In pattern and colour, ssp. *gigas* is very similar to ssp. *virgo*, but *gigas* is much larger overall (with the wing area often two to three times greater than that of ssp. *virgo*) and the hindwing colours are often brighter or more saturated, particularly in comaprison to boreal *G. virgo* populations. The genetic differentiation of *G. v. gigas* is discussed under 'Molecular Variation' for *G. virgo*.

Description

Head - Palps black, frons and vertex yellowish to creamy buff; male antennae moderately bipectinate, pectinations averaging 7.75×10^{-1} mm, ($n = 2$); female antennae slightly bipectinate; dorsal scales dark brown to black with scattered buff scales; eyes well-developed. ***Thorax*** - Vestiture black with yellowish to creamy buff borders on vertex, patagia and tegulae; entirely dark brown to black ventrally, including legs. ***Abdomen*** - Dorsal ground colour pinkish orange; apex pale buff; medial and lateral markings black; medial band relatively broad; ventrally usually entirely black, sometimes with traces of pale buff along midline at distal margins of segments. ***Forewing*** - Length averaging 29.2 mm ($n = 3$); black dorsally, vein lines complete, lines and bands yellowish buff to creamy buff; antemedial band usually absent, or visible as slight pale bar along costa; postmedial band variable, most often present as rectangular bar across discal cell onto costa, rarely extending slightly beyond cubital vein; postmedial and subterminal bands well developed; postmedial angled strongly at M_3, not extending through postcubital stripe; fringe, costa and anal margin concolourous with pale markings; ventral markings similar, but dark markings slightly paler, and with a disinct yellowish cast overall; sexes similar, with females slightly larger. Hindwing - Ground colour orange to pinkish-orange; black markings well developed; antemedial spots consisting of costal, discal and anal spots, discal spot nearly always present and well-developed; postmedial and subterminal spots well developed, not confluent except near tornus; ventral markings similar, but colours more washed-out and with overall yellowish cast; sexes similar. *Genitalia:* larger overall than *G. v. virgo*, but otherwise indistinguishable.

Distribution

The range of this subspecies is centered on the southeastern USA, including the Great Smoky Mountains of TN and NC, and occuring south to GA and northern FL. The northern limits of this taxon, and the relationship to ssp. *virgo*, should be looked at in more detail. Nominate *G. virgo* occurs in the Great Lakes region and New England, presumably grading into ssp. *gigas* along the Atlantic coastal plain and the Applachian mountains.

GRAMMIA ANNA (GROTE)

FIGS. 2-9, 2-46, 2-102.

Arctia anna Grote, 1863 [1864]: 335.
Arctia persephone Grote, 1864: 433.
Apantesis anna (Grote); Franclemont, 1983: 117.
Grammia anna (Grote); Ferguson and Opler 2006: 9.

Type Material

Arctia anna: described from a female holotype, type no. 7685 in ANSP [not examined]; the type locality is Pennsylvania.

Arctia persephone: described from a male holotype, type no. 6886 in ANSP [not examined]; the type locality is Pennsylvania.

Diagnosis

The broad black hindwing borders and lined forewings with prominent postmedial (and often medial) bands are usually sufficient to recognize *G. anna*. Rare forms of *G. anna* with reduced forewing bands may resemble large *G. virguncula*, but *G. anna* never has a thick-lined cubital vein, and vein Cu2 is continuous with or barely separated from the postcubital stripe in *G. anna*, while in *G. virguncula* Cu2 remains well separated from the postcubital for its entire length.Yellow forms of *G. virgo* and *G. parthenice* lack the broad suffused hindwing markings characteristic of *G. anna*.Yellow forms of *G. ornata* can be separated by the lack of transverse band extensions beyond the postcubital stripe, and the fact that they occur on opposite sides of the continent in vastly different habitats.

Description

Head - Palps black, frons and vertex yellowish buff; male antennae moderately bipectinate, pectinations averaging 4.53×10^{-1} mm, ($n = 6$); female antennae slightly biserrate; dorsal scales dark brown to black, varying to predominantly yellowish buff; eyes well-developed. ***Thorax*** - Vestiture black with yellowish buff borders on vertex, patagia and tegulae; patagia rarely entirely buff; entirely black ventrally, or with yellowish tuft at base of forecoxa; legs entirely or predominantly black, tibia yellowish laterally. ***Abdomen*** - Dorsal ground colour yellow, apex black; medial and lateral markings black; medial band relatively broad; pale buff ventrally, lateral black markings broad, often confluent such that ventrum is entirely black. ***Forewing*** - Male forewing length averaging 20.1 mm ($n = 6$ males); black dorsally, vein lines complete, lines and bands yellowish buff to whitish buff; antemedial band reduced to wide spot at costa or absent; medial band restricted to discal bar, sometimes reduced to line or absent entirely; postmedial band well developed, angled strongly at M_3, very rarely reduced or absent; subterminal band well developed; fringe and anal margin concolourous with pale markings, costal margin entirely pale, somtimes only to subterminal band; ventral markings similar, but dark markings with a paler yellowish cast; sexes similar. Hindwing - Ground colour yellow, black markings highly variable in extent; antemedial spots when present streaked basad; medial spot usually large and prominent; postmedial and subterminal elements usually confluent into one broad band, postmedials virtually never discrete; ventral markings similar, but dark markings with a paler yellowish cast; sexes similar, although females generally with more extensive dark markings, sometimes black entirely. ***Male genitalia*** - Distal portion of valve gradually tapering to rounded apex; saccular extension poorly developed, saccular process reduced; uncus broad-based, process evenly tapered to point, 3 × as long as width of base; juxta 1.5 – 2 × wider than height; aedeagus with dorsad curve at ⅔ distance beyond base; vesica with basal and medial chamber approximately equal in length and width, not scobinate; second medial diverticulum elongate, prominent; distal chamber relatively large, 2.5 × as long as width of medial chamber, kidney-shaped, minutely scobinate; vesica as long as or slightly shorter than aedeagus. ***Female genitalia*** - Not examined.

Biology

Adult collection dates indicate a single flight period between late May and late June. *Grammia anna* inhabits relatively rich, mesic wooded areas, and is one of only a few species restricted to habitats associated with deciduous forests of eastern North America.

Distribution

Southern Ontario and New England south to Georgia. Smith (1938a) records it from as far west as eastern Nebraska (Fig. 2-102).

Molecular Variation

Six specimens of *G. anna* from four localities (ON, QC, GA, NC) all exhibited unique haplotypes, at least 4.9% divergent from all other *Grammia* haploptypes (Table 2-2, Fig. 2-99).

GRAMMIA PARTHENICE (KIRBY)

FIGS. 2-10, 2-47, 2-78, 2-103.

Callimorpha parthenice Kirby, 1837: 204.
Arctia saundersii Grote, 1864: 75, pl. 4 f. 3.
Arctia intermedia Stretch, 1873 [1874]: 216.
Arctia stretchii Grote, 1875: 197.
Arctia approximata Stretch, 1885: 104.
Arctia intermedia var. *circa* Stretch, 1906: 120, pl. 5 f. 26.
Apantesis parthenice (Kirby); Franclemont 1983: 117.
Apantesis parthenice intermedia (Stretch); Franclemont 1983: 117.
Grammia parthenice (Kirby); Ferguson and Opler 2006: 9.
Grammia parthenice intermedia (Stretch); Ferguson and Opler 2006: 9.

Type material

Callimorpha parthenice: described from an unstated number of types from "North America"; since there are no known extant types of taxa described by Kirby (1937), the following **neotype** is designated to ensure the stability of the name: "CAN[ADA]: AB [Alberta] Chauvin, 13km N/ 52.810N 110.106W/ 25-vii-04 C. Schmidt/ sand dune parkland", "NEOTYPE/ Callimorpha/ parthenice Kirby/ B.C. Schmidt 2007". A number of taxa described by Kirby (1837) were collected by the Franklin expedition in present day Saskatchewan and northern Alberta, Canada, and the neotype is therefore selected from the same region.

Arctia saundersii: described from an unstated number of specimens, a male syntype in ANSP (type no. 7688) [not examined]; the type material was collected in "Canada West", present-day southern Ontario, Canada. Hampson (1901) lists five male specimens in the Grote collection from Renfrew Co., Canada. The **type locality** of *Arctia saundersii* is therefore restricted to Renfrew County, Ontario, Canada to ensure the stability of the name for this geographically variable species.

Arctia intermedia: described from an unstated number of specimens from Texas, [USA]. The probable male holotype is in CAS, type no. 3245 [not examined].

Arctia stretchii: described from Texas [USA]; the male holotype is in USNM, type no. 33682 according to Smith (1938a) [not examined]. Based on a variant of *parthenice* that exhibits a complete antemedial band.

Arctia approximata: described from a single female specimen from "Canada" [CAS, not examined]; The illustration in Stretch (1906, plate 8 fig. 10) is likely of the type. Although the vague reference to "Canada" in the 1885 description could apply to much of present-day Canada, it is seems most likely that the type material of *approximata* originated from the relatively well known territory of southern Ontario ("Canada West" prior to confederation in1867); in order to stabilize the name *approximata*, the **type locality** is hereby restricted to Ottawa, Ontario, Canada.

Arctia intermedia var. *circa*: named based on an indication to an illustration, with no given type locality or known extant types; *circa* is an unavailable infrasubspecific name. The illustration in the original description is diagnostic, and is a variant of *G. parthenice*.

Diagnosis

Most similar to *G. virgo*, but *G. parthenice* lacks any trace of the antemedial spots on the hindwing that are so prominent in *virgo*; the cubital vein is thin-lined in *G. parthenice*, thick in *G. virgo*.

Description

Head - Palps black, frons and vertex yellowish buff; male antennae moderately bipectinate, pectinations averaging 4.03×10^{-1} mm, ($n = 6$); female antennae slightly to strongly biserrate; dorsal scales dark brown to black; eyes well-developed. ***Thorax*** - Vestiture black with pale to yellowish buff (rarely pinkish buff) borders on vertex, patagia and tegulae; entirely black ventrally, rarely with buff scales at base of forecoxa; legs entirely or predominantly black, tibia rarely buff laterally. ***Abdomen*** - Dorsal ground colour yellow-orange to orange-pink, apex black, rarely buff; medial and lateral markings black; medial band varying from thin to broad; buff ventrally, lateral black markings varying from lateral rows of spots to largely or entirely confluent, often entirely black. ***Forewing*** - Male forewing length geographically variable, ranging from 16.5 mm to 27 mm, females averaging slightly larger; black dorsally, vein lines complete, lines and bands yellowish buff to whitish buff, rarely pink or pinkish buff; antemedial band usually reduced to wide spot at costa or absent, sometimes complete and extending to anal margin; medial band usually well developed and restricted to discal bar, sometimes extending to postcubital stripe or beyond; postmedial band well developed, angled slightly at M_3, rarely reduced or absent; subterminal band well developed; fringe and anal margin concolourous with pale markings, costal margin entirely or (rarely) partly pale; ventral markings similar, but dark markings slightly paler, pale areas with distinct yellow cast; sexes similar, but females with slightly more elongate wing shape. Hindwing - Ground colour orange-pink to deep pink, particularly in females; black markings variable in extent; antemedial spots never present; medial spot usually large and prominent; postmedial and subterminal elements varying from very reduced to broad and confluent, particularly at tornus; ventrally with paler dark markings and ground colour washed out and yellowish; sexes similar. ***Male genitalia*** - Distal portion of valve gradually tapering to rounded apex; saccular extension poorly to moderately developed, saccular process moderately developed; uncus broad-based, process evenly tapered to point, 2-3 × as long as width of base; juxta 1.5 – 2 × wider than height; aedeagus with dorsad curve at ⅔ distance beyond base; vesica with basal and medial chamber approximately equal in length and width, not scobinate; distal chamber twice as long as width of medial chamber, relatively narrow, elongate; vesica slightly shorter than aedeagus. ***Female genitalia*** - Ductus bursae unsclerotized, slightly constricted medially; corpus bursae globose, 3 × width of ostium bursa; signa round to slightly elliptical; signa finely scobinate; coil of appendix bursae evenly rounded; posterior apophysis 2.5 × longer than papillae anales.

Biology

Grammia parthenice is univoltine, with adult collection dates range from late June to early October; northern and Rocky Mountain records are primarily from mid July to early August. Collection dates for the eastern U.S., at least as far north as Pennsylvania and Massachusetts, are for September, and into October for North Carolina, Georgia and west to Texas. *Grammia parthenice* inhabits a wide variety of ecoregions and habitats, from rich deciduous forests to the grasslands of the Great Plains, preffering mesic meadows, pastures and edges of wetands.

Distribution

The most widespread species of *Grammia*, occuring from central British Columbia east to Newfoundland (Morris 1980), south to Georgia in the east, west to Texas, Utah and Montana (Fig. 2-103).

Molecular Variation

Twenty specimens of *G. parthenice* from ten localities across the species' range segregated into nine haplotypes of two highly divergent lineages, resulting in up to 3.5% intraspecific divergence (Table 2-2). Haplotypes of the Parthenice lineage (Fig. 2-132) formed a monophyletic group, but haplotypes of the Eastern lineage (Fig. 2-134) were shared with or very similar to those of other species in the Eastern lineage. As discussed in Chapter 3, Eastern lineage haplotypes likely represent introgression of non-conspecific mtDNA into *G. parthenice* populations. Haplotypes of the Parthenice lineage were restricted to eastern North America (QC, KY, NC, GA), while Eastern haplotypes occured throughout the northern portion of the species' range.

Remarks

Although *G. parthenice* is superficially most similar to *G. virgo*, molecular data did not suggest a close relationship between these species. The numerous phenotypical and physiological differences also do not support a close relationship between *G. parthenice* and *G. virgo*. The phenotypic differences are given above in the diagnosis; the fact that *G. virgo* flies in mid summer while *G. parthenice* flies in late summer / early fall is indicative of physiological differences. Shared haplotypes between *G. parthenice* and *G. virguncula* may indicate a closer relationship between these species, but they differ in forewing pattern (presence of transverse bands and finer vein lines in *parthenice*), hindwing colour and pattern (pink-orange not yellow, never melanic; lacking basal dark markings) abdomen colour and pattern (pink-orange, last 2 segments sometimes entirely black), and the relatively shorter antennal pectinations (relative to body size), larger size and earlier flight period of *parthenice*. *Grammia parthenice* and *G. virguncula* occur sympatrically over most of eastern North America, and I have not seen phenotypically intermediate specimens which could be attributed to hybridism.

G. parthenice is one of the most variable members of the genus in terms of size, colour, pattern and genitalic structure. Although there is some geographic structure to this variation, much of it is also exhibited within populations. Specimens from the southeastern U.S. often have wingspans more than twice that of the northern plains and boreal populations, and have been referred to as subspecies *intermedia* (Franclemont 1983, Ferguson and Opler 2006); this name was based on type material from Texas, so it may not apply to the eastern and southeastern populations. This geographic variation should be re-evaluated with more study material.

GRAMMIA VIRGUNCULA (KIRBY)

FIGS. 2-11, 2-49, 2-79, 2-104.

Callimorpha virguncula Kirby, 1837: 304.

Euprepia virguncula var. *otiosa* Neumögen and Dyar, 1893: 142.

Arctia speciosa Möschler, 1864: 195. **revised status**

Apantesis virguncula (Kirby); Franclemont 1983: 117.

Apantesis virguncula speciosa (Möschler); Franclemont 1983: 117.

Grammia virguncula (Kirby); Ferguson and Opler 2006: 9.

Grammia speciosa (Möschler); Ferguson and Opler 2006: 9.

Type Material

Callimorpha virguncula: Described from an unstated number of specimens from "Canada"; Kirby's type specimen(s) is presumed lost, as there are no known extant types of any of the taxa described by Kirby in 1837, including several butterfly species (Miller and Brown 1981) and two plusiine noctuids (Lafontaine and Poole 1991); in order to stabilize the nomenclature of this species complex, the following **neotype** is designated: "Canada, Ontario,/ Carp Ridge, E side/ 45 24.63'N 76 03.45'W/ 28 June 2003/ J. Troubridge Le.g.", "NEOTYPE/ Callimorpha/ virguncula Kirby/ B.C. Schmidt 2007" [CNC].

Euprepia virguncula var. *otiosa*: the name is based on two abberant specimens of *virguncula* which show traces of transverse bands, and *otiosa* is therefore an unavailable infrasubspecific name.

Euprepia speciosa: described from one female and two male syntypes from Labrador, [Canada]. A male syntype [FMNH] labelled "Arctia Speciosa/ Labrador Möschl./ orig. Type H.B. Möschler", "Labrad./ Hf. R./ 72." Arctiidae/ genitalia slide/ No. 1221", "Lectotype ♂/ det. A. Watson 1966", "Lepidoptera Type/ Photograph No. 198/ Field Museum", "LECTOTYPE/ Arctia/ speciosa Möschler/ B.C. Schmidt 2007" is hereby designated **lectotype** to stabilize the name. This specimen was noted by Smith (1938a) and likely also Strecker (1899) as a female; it is a male specimen with glued-on female antennae [photo examined].

Diagnosis

Grammia virguncula is most similar to *G. kodara, G. philipiana* and *G. quenseli*. *G. virguncula* and *G. kodara* do not occur together, and the differences between these taxa are discussed under *G. kodara*. Compared to *G. philipiana, G. virguncula* has yellow hindwings, not orange, longer male antennal branches, and normal, not reduced, eyes. *G. quenseli* has pale (not black) antennae with much shorter pectinations, reduced eyes, and entirely black or grey and pale yellow hindwings, not bright yellow as in *G. virguncula*. Forms of *G. virguncula celineata* lacking the forewing vein lines can be similar to *G. elongata,* but the antennal branches are much shorter, and the eyes are not reduced compared to *G. elongata*. *Holarctia obliterata* is superficially similar, but has better developed forewing costal bars, in addition to the substantial genitalic differences discussed under that species and the discussion of the genus *Holarctia*.

Description

Head - Palps black, frons and vertex pale to yellowish buff, vertex rarely black centrally; male antennae moderately bipectinate, pectinations averaging 4.00 × 10^{-1} mm, (*n* = 29 males); female antennae moderately to strongly biserrate; dorsal scales dark brown to black; eyes well-developed to slightly reduced, mean diameter 8.2 × 10^{-1} mm . ***Thorax*** - Vestiture black with pale to yellowish buff borders on vertex, patagia and tegulae; black ventrally, base of coxa and distal area usually with yellowish buff scales; coxa and femur black centrally, yellow at base and apex, giving striped appearance, or entirely dark brown - black; tibia and tarsus pale buff dorsally, black ventrally. ***Abdomen*** - Dorsal ground colour yellow, pale buff near apex; medial and lateral markings black; pale buff ventrally, lateral black markings broad but not confluent at midline; occasionally entirely dark brown – black ventrally and dorsally in ssp. *celineata*. ***Forewing*** - Male forewing length averaging 16.2 mm (range 13.9 – 20.5 mm, *n* = 15 males), largest for populations from the Great Lakes region and southwestward, smallest for *speciosa* form; black dorsally, vein lines complete (except for ssp. *celineata*, where lines vary to absent), lines and bands yellowish buff to pale whitish buff; cubital vein line often broader than other vein lines; all bands except subterminal usually absent, medial band very rarely present as bar in discal cell; fragmentary postmedial band sometimes present, but only in ssp. *celineata*; subterminal band complete; fringe and anal margin concolourous with pale markings, costal margin entirely pale, sometimes reduced to basal half; ventral markings similar, but dark markings with a paler yellowish cast; sexes similar. Hindwing - Ground colour yellow, black markings highly variable in extent, but antemedial, medial, postmedial and subterminal elements nearly always present; antemedial elements usually as streaks or dashes extending to base; spots often discrete in ssp. *virguncula*, largely confluent and expanded in ssp. *speciosa*, varying to entirely black in ssp. *celineata*; ventral markings similar, but dark markings with a paler yellowish cast; sexes similar. ***Male genitalia*** - Distal portion of valve gradually tapering to rounded or slightly pointed apex; saccular extension poorly to moderately developed, saccular process moderately developed; uncus broad-based, process evenly tapered to point, 2-3 × as long as width of base; juxta 1.5 – 2 × wider than height; aedeagus with dorsad curve at ⅔ distance beyond base; vesica with basal and medial chamber approximately equal in length and width, not scobinate; distal chamber medium-sized, twice as long as width of medial chamber, kidney-shaped, roughly scobinate; vesica as long as or slightly shorter than aedeagus. ***Female genitalia*** - Ductus bursae unsclerotized; proximal half of ductus bursae twice as wide as distal half; corpus bursae more or less globose, 4x width of ostium bursa; signa round to slightly elliptical, relatively small averaging about 1.97×10^{-1} mm; signa coarsely scobinate; coil of appendix bursae evenly rounded; posterior apophysis 1.5 – 2 × longer than papillae anales.

Biology

The peak flight period is from mid June to late July, with extreme dates spanning late May to late August. *Grammia virguncula* occurs in a variety of open wooded habitats, ranging from marshes, fens and bogs to transition parkland. Despite this apparent range of suitable habitats, *virguncula* is usually not common. Adults come to light, with the exception of ssp. *celineata*, and possibly the far northern populations.

Distribution

Occurs across most of northern and central North America, from Alaska south along the Rocky Mountains and northern Great Plains to Arizona (Ferguson *et al.* 2000), Wyoming, and Nebraska. In the east, found from Newfoundland (Morris 1980) south at least to Missouri, Michigan, Pennsylvania and New Jersey.

Molecular Variation

Grammia virguncula exhibited 23 haplotypes among 53 sampled individuals, from 25 localities across most of the species' range (Table 2-2). Much of the Eastern lineage consisted of *G. virguncula* haplotypes, and only one *G. virguncula* haplotype fell outside this lineage (VR1, Western lineage: Fig. 2-133). Fifteen of 23 haplotypes were unique to *G. virguncula,* although most of these differed by only one or two bp from haplotypes occuring in other species (Table 2-2). Species sharing haplotypes with *virguncula* included *G. williamsii, G. parthenice, G. elongata* and *G. margo*, all within the Eastern lineage. As discussed in Chapter 3, the Eastern lineage is most likely native to *G. virguncula*, with multiple hybridization events resulting in taxonomically extensive introgression of Eastern haplotypes into other species. Despite extensive haplotype sharing, there is genetic evidence (Chapter 3) that the phenotypically distinct Atlantic maritime populations are unique. Due to the complex genealogy, the currently available molecular data are insufficient to resolve any potential genetic differentiation of *virguncula* subspecies discussed below.

Remarks

The species most closely related to *Grammia virguncula* appear to be *G. quenseli* and *G. philipiana,* and to a lesser extent *G. parthenice.* As discussed under the *G. virguncula* subspecies accounts, there is a tendency towards melanism and reduction in size in northern boreal and bog populations of *virguncula*, resulting in a similarity to *G. quenseli*. The two taxa remain distinct, however, where they co-occur, with diagnostic antennal structure, antennal colour, eye size and wing markings. The limited biological data on northern *G. virguncula* populations show that it is a species of peat bogs, while *G. quenseli* prefers dry rocky tundra. Similarly, the morphological differences between *G. virguncula* and *G. kodara* and *G. philipiana* leave little doubt that *virguncula* is a distinct from the aforementioned species.

Populations from Nebraska east to the Great Lakes region are larger and tend to show more reduced hindwing dark markings (Fig. 11e) in comparison to other *virguncula* populations, and should perhaps be considered as a subspecies distinct from those currently recognized.

GRAMMIA VIRGUNCULA VIRGUNCULA (KIRBY)

FIGS. 2-11A, B.

Diagnosis

Compared to other *G. virguncula* subspecies, the nominate subspecies is relatively large, exhibits well-marked forewing vein lines with a broad cubital line, and very rarely exhibits traces of transverse bands other than the subterminal band. Some populations from the southern Great Lakes and eastern Great Plains are larger and more brightly coloured, and may be a separate subspecies.

Distribution

Nova Scotia west to Alberta, south to Arizona (Ferguson *et al.* 2000), Missouri, Michigan, Pennsylvania and New Jersey. The taxonomic status of Great Lakes/New England bog populations are not certain, and are discussed under 'Remarks' for *G. virguncula speciosa.*

GRAMMIA VIRGUNCULA SPECIOSA (MÖSCHLER), REVISED STATUS

FIGS. 2-11C, D.

Diagnosis

In comparison to *G. v. virguncula*, susbspecies *speciosa* is smaller overall, has a more elongate forewing shape, and has a thin, not thick-lined cubital vein; the hindwing black markings are usually more extensive. See 'Diagnosis' under *virguncula* for comparison to similar species.

Biology

Adult collecting records range from late June to late July, and the species occurs in wetlands, bogs and subarctic tundra. Adults may fly by day, and are also attracted to light. The immature stages are unknown.

Distribution

Labrador west to northern Alberta.

Remarks

Ferguson (1985: 229) stated that he thought *speciosa* was a species distinct from *G. virguncula*, but did not go into further detail on this matter and retained *speciosa* as a subspecies of *G. virguncula*, as indicated by the figure caption on p. 266 (Ferguson 1985). Subsequently, *speciosa* was treated as a valid species in Ferguson *et al.* (2000) and Ferguson and Opler (2006). Ferguson *et al.* (2000) treated all western North American populations as speciosaClearly, Ferguson thought *speciosa* to be specifically distinct, but without providing supporting data, and without indicating the revised taxonomic status in either work. The populations of smaller, often darker specimens occuring in bog habitats of New England and the Great Lakes region have subsequently been treated as *G. speciosa* by some (e.g. Ferge and Balogh 2000), and *G. speciosa* is listed as an endangered species in Connecticut (Connecticut Department of Environmental Protection, 2004). I have not found any consistent morphological differences between the smaller bog form and typical form in the Great Lakes region, and no evidence of strictly sympatric populations of the two taxa. A comparison of long series of specimens from upland mixedwood forest (Carp Ridge) and peatland habitat (Mer Bleue bog) in the Ottawa area of Ontario shows continuous variation from somewhat smaller specimens with extensive dark hindwing markings, to slightly larger, paler specimens. In Alberta, specimens from boreal bogs and fens are indistinguishable from prairie grassland and aspen parkland sites. There is considerable variation in eye diameter and antennal branch length within *virguncula*, but these traits vary continuously without forming distinct groups within a geographic region. Specimens from Nebraska show the greatest wing length, eye diameter and antennal branch length, with a gradual decrease in size northward and westward; this trend is evident even within series of Alberta material from the northern praries through the parkland and into the boreal region. In the great Lakes region and New England, size/colour variation occurs at finer geographic scales, which I interpret as phenotypic variation driven by habitat conditions and microclimate, i.e. cooler wetland habitats such as bogs induce *speciosa* phenotypes. Based on the available evidence, the Great Lakes / New England "*speciosa*" populations are therefore best treated as conspecific with *G. virgunucla*.

Regardless of the taxonomic status of the Great Lakes / New England *virguncula* populations, the identity of nominate *speciosa* should be clarified. The lectotype specimen from Labrador has a thin-lined cubital vein, not thick lined as in nearly all of the northeastern North American material I have examined, and the forewing shape is narrower than nominal *virguncula*. Interestingly, Morris (1980) remarks that Labrador *virguncula speciosa* are more narrow-winged than Newfoundland *virguncula*, also suggesting the taxon occuring in the Atlantic provinces and states is not true *speciosa*; this is certainly true of Nova Scotia populations (Guysborough, Shelby, Hants, and Kings Counties), which have a shorter, broader wing shape and relatively broad, yellowish vein lines, and in this respect are more similar to ssp. *virguncula*. The Nova Scotia populations commonly occur in bog habitats. For the reasons outlined above, I am restricting the application of the name *speciosa* to northern boreal populations, from Labrador west to at least northern Alberta (Birch Mountains); *speciosa* is structurally most similar to ssp. *celineata* (reduced antennal branches and eyes, tendency for dark hindwings), and the two presumably intergrade along the eastern edge of the MacKenzie and Rocky Mountains, but very little material is available from these regions.

GRAMMIA VIRGUNCULA CELINEATA SCHMIDT, NEW SUBSPECIES

FIGS. 2-11F, G.

Callarctia celia form *lineata* Smith, 1938b:10 (unavailable infrasubspecific name).

Type Material

Holotype **-** ♂. Canada, Alberta, [southwest of] Calgary, Near Billings Lumber Mill [head of Fish Creek, 12 km SW of Bragg Creek], 26 June 1898, F.H.W. Dod [CNC] [Note: the location of Billings Lumber Mill was restricted to the head of Fish Creek by Kondla (1996)]. ***Paratypes*** -18 ♂♂, 11 ♀♀ **Alberta**: 4 ♂♂ 1♀, same data as holotype [CNC]; 1♂, same locality as holotype, 19 June 1898 [CNC]; 2♂♂ 1♀, Bragg Creek, 29 June 1974, F. Sperling [USNM]; 1♂ Bragg Creek, 28 June 1974, F. Sperling [USNM]; 1♂, Bragg Creek, 12 July 1972, F. Sperling [USNM]; 1♀, Bragg Creek, 4 July 1972, F. Sperling [USNM]; 1♂, Spruce bog, Nitchi Cr., 31-6-W5, 24 June 1990, C. Schmidt [BCSC]; 1♀, 16 mi. W of Water Valley, 14 July 1990, D. Lawrie [UASM]; 1♂, Junction Mtn. trail, 26 August 2000, E.M. Pike [UASM]; 3♀, Nordegg, 24 July 1918, 20 June 1926, 16 July 1938, K. Bowman [UASM]; 1♂, Adams lookout, 11 July 1982, E.M. Pike [UASM]; **British Columbia:** 1♀, Atlin, 2200', 21 June 1955, H. Huckel [CNC]. **Northwest Territories:** 1♂, Cameron Bay, Great Bear L., 8 July 1937, T. N. Freeman [CNC]. **Yukon:** 1♀, Klondike R., 2000', 20 July 1919 [CNC]; 1♂, Mt. Archibald, 6500', St. Elias Range, 23 June 1991, J. Troubridge [UASM]; 1♂, La Force L., 3300', 28 June 1960, J.E.H. Martin [CNC]. **Alaska:** 1♂, Suslota L., 3 July 1975, H. Hawkins [USNM]; 1♂, vic. of Fairbanks, 10-24 June 1973, H. Bates [USNM]; 1♀, Ramparts, 16 June 1923 [USNM]; 1♀, Chena Ridge, nr. College, June 1975, K.W. Philip [USNM].

Etymology

Grammia virguncula celineata is a combination of the names *celia* and *lineata*, the name originally proposed for this taxon by Smith (1938a,b).

Diagnosis

G. virguncula celineata is unique among *virguncula* populations in that the abdomen and hindwing can be entirely black, the forewing vein lines can be reduced or absent, and forms expressing fragmentary medial and postmedial bands are more common. The limited available data show that *G. v. celineata* is diurnal. Forms exhibiting both loss of vein lines and expression of forewing bands can be similar to *G. margo*, but *celineata* has larger eyes, longer antennal pectinations, is larger overall and flies later in the year (mid June onwards vs. late May to early June) compared to *margo*. See diagnosis under *G. virguncula* for comparison to other species.

Description

Head - Palps black, frons and vertex pale to yellowish buff; male antennae moderately bipectinate, pectinations averaging 3.18×10^{-1} mm, ($n = 8$); female antennae moderately biserrate; dorsal scales dark brown to black; eyes slightly reduced, mean diameter 7.1×10^{-1} mm. ***Thorax*** - Vestiture black with pale to yellowish buff borders on vertex, patagia and tegulae; black ventrally, base of coxa and distal area usually with yellowish buff scales; coxa and femur black centrally, yellow at base and apex, giving striped appearance, or entirely dark brown - black; tibia and tarsus pale buff dorsally, black ventrally. ***Abdomen*** - Dorsal ground colour yellow, pale buff near apex; medial and lateral markings black, medial line broad; pale buff ventrally, lateral black markings broad but not confluent at midline; occasionally entirely black ventrally and dorsally. ***Forewing*** - Male forewing length averaging 15.1 mm ($n = 6$ males); black dorsally, vein lines complete; reduced to distal half, or absent; lines and bands yellowish; rarely pale buff; cubital vein line not thickened; medial band usually absent, occasionally present as bar in discal cell; fragmentary postmedial band often present as bar across distal end of discal cell, and/or below end of discal cell; subterminal band complete; fringe and anal margin concolourous with pale markings, costal margin entirely pale, somtimes reduced to basal half; ventral markings similar, but dark markings with a paler yellowish cast; sexes similar. Hindwing - Ground colour dull yellow or entirely black; black markings highly variable in extent, but antemedial, medial, postmedial and subterminal elements nearly always present, and often confluent to the point where yellow is reduced to irregular central area; entirely black form relatively common in both sexes (seven of 30 specimens); ventral markings similar, but dark markings with a paler yellowish cast; sexes similar. *Genitalia:* not distinguishable from *G. virguncula* structurally; see description under *G. virguncula*.

Biology

Collection dates for *G. v. celineata* range from mid June to August, with most records from late June. Although the eyes are not strongly reduced in size, *G. v. celineata* males fly in late afternoon in spruce bogs, and are not known to come to light (BCS, pers. obs.).

Distribution

Occurs from southwestern Alberta north to Alaska, Yukon and the Northwest Territories.

Remarks

This taxon was associated with *G. margo* and *G. franconia* (as *G. celia* of auth.) by Smith (1938a,b), who believed it to be a form of *"celia"* with lined forewings. Examination of additional specimens from the vicinty of the type locality show variation to typical *virguncula* wing pattern in specimens collected at the same locality and the same date as unlined forms. The antennal structure, eye size, habitat and flight time is also consisitent with *virguncula (sensu lato)*, and inconsistent with the *margo / franconia* group. The relationship of *G. v. celineata* to other *G. virguncula* populations is unclear – typical *G. virguncula* occurs in prairie and montane regions adjacent to populations of *G. v. celineata* in the Alberta foothills, but there is no evidence that the two taxa occur in strict sympatry, which would suggest that *G. v. celineata* is a distinct species. The relationship between *celineata* and nominate *virguncula* may prove to be parallel to the *virguncula-speciosa* situation as discussed under *G. v. speciosa*, and indded that *G. v. celineata* and *G. v. speciosa* are conspecific but specifically distinct from *G. v. virguncula*. The situation awaits further study.

Although this taxon was first collected over a cerntury ago by Alberta's foremost pioneer lepidopterist, Frederic H. Wolley Dod, its taxonomic affinity has remained unclear (and perhaps still is!). The phenotypes expressed by *G. v. celineata*, particularly evident in a series of specimens from the foothills of southwestern Alberta, may be indicative of introgression with other *Grammia* species, a well-documented phenomenon for the Old World Swallowtail group in this region (Sperling 1987).

GRAMMIA KODARA DUBATOLOV AND SCHMIDT

FIG. 2-12.

Grammia kodara Dubatolov and Schmidt, 2005: 53.

Type Material

Holotype male from Mezhded', Sul'ban River, Kodar Station, Kodar Range, Chita Province, Russia [SZM]; male and female paratype in USNM [examined].

Diagnosis

Grammia kodara is most similar to *G. quenseli*, *G. philipiana* and *G. virguncula*. However, in *kodara* the broad longitudinal line between the cubital and anal vein of the forewing does not usually reach the distal margin; the dark smokey hindwing colour also distinguishes *G. kodara* males from those *G. virguncula* and *G. philipiana*. *Grammia quenseli* is smaller overall with more reduced eyes, shorter male antennal pectinatiosn and pale not black antennae. Internally, the long male vesica of *G. kodara* is unique within this group. *Holarctia obliterata* is superficially similar, but has a yellow or yellow-orange rather than dusky hindwing, in addition to the substantial genitalic differences discussed under *Holarctia*.

Description

Head - Palps black or yellowish buff, frons yellowish buff, vertex black centrally, yellowish buff along sides; male antennae moderately bipectinate, longest pectinations relatively short (2.96×10^{-1} mm, $n = 1$ male); female antennae moderately biserrate; dorsal scales black; eyes strongly reduced and elliptical (diameter $= 6.11 \times 10^{-1}$ mm, $n = 1$ male); gena exposed at eye margins. ***Thorax*** - Vestiture black with relatively narrow, yellowish buff borders on vertex, patagia and tegulae; black ventrally, coxa and femur black centrally, yellow at base and apex, giving striped appearance; tibia and tarsus pale buff dorsally, black ventrally. ***Abdomen*** - Dorsal ground colour yellowish, pale buff near apex; medial and lateral markings black; black ventrally, abdominal segments bordered yellowish buff distally. ***Forewing*** - Male, forewing length 12-16.5 mm (male), 17-19.8

mm (female); black dorsally, vein lines complete, yellowish white; postcubital line not reaching distal margin; basal and antemedial band absent; medial band usually restricted to discal cell; postmedial band absent or restricted to discal cell; subterminal band reduced or complete; fringe, anal margin and basal two-thirds of costal margin yellowish, concolourous with remainder of line markings; ventral markings similar, slightly more diffuse. Hindwing - Ground colour yellow or entirely grey, black markings well developed, often confluent; antemedial markings smeared basad; ventrally, pale medial area brighter than dorsal side, lacking cast of dark grey scales. ***Male genitalia*** - Distal portion of valve gradually tapering to rounded apex, slightly curved ventrocaudad; saccular extension poorly developed, saccular process reduced; uncus broad-based, process evenly tapered to point; juxta roughly equally high as wide; aedeagus with dorsad curve at ⅔ distance beyond base; vesica with basal and medial chamber approximately equal in length and width; distal chamber relatively large, kidney-shaped; vesica overall longer than aedeagus. ***Female genitalia*** - Not examined.

Biology

Adult collection dates range from mid June to mid July. This species is only known from the type series, and the apparent rarity may be due to the diurnal activity of the adults as indicated by the extremely reduced eyes. The immature stages unknown.

Distribution

So far recorded only from the vicinity of the type locality in the Kodar Mountain Range east of Lake Baikal, Chita Province, Russia.

Molecular Variation

Two sequenced specimens showed very similar haplotypes with a minimum interspecific divergence of 2.7% (Table 2-2). Three other haplotypes, one each of *G. quenseli*, *G. williamsii* and *G. virgo* (QE1, WI1, VI14, or 'QWV'), were most similar to *G. kodara*, together forming the Kodara lineage (Fig. 2-132). The QWV haplotypes were highly divergent from the remainder of these species' haplotype complements, but the significance of this is unclear. The morphological and ecological data suggest *G. quenseli* could be the sister species to *G. kodara* (see 'Phylogeny' at end of section), in which case QWV may represent the native, or at least an ancient, lineage of *G. quenseli* with introgression into *G. wiliamsii* and *G. virgo*. Additional sampling would be required to test this hypothesis.

Remarks

This is the only species of *Grammia* that is known to be restricted to the Palaearctic region.

GRAMMIA PHILIPIANA FERGUSON

FIGS. 2-13, 2-105.

Grammia philipiana Ferguson, 1985: 229, f. 53, 54.
Grammia olga Dubatolov, 1990: 79, f. 1, 2.
Grammia philipiana Ferguson; Ferguson and Opler 2006: 9.

Type Material

Grammia philipiana: described from a male holotype [USNM; examined], female allotype [USNM; examined], and a female paratype [CNC; examined]; the type locality is Ray Mountains, near Torment Creek, 65° 51.5' – 52'N, 151° 25-27'W, Alaska, USA.

Grammia olga: described from a male holotype, female allotype, and three male paratypes [ZMUM?; photo examined]; the type locality is the "lower reaches of the Gusinaya River, Wrangel Island, [Russian Federation]" according to Murzin (2003).

Diagnosis

G. philipiana could possibly be mistaken for *G. virguncula* or *G. quenseli*, but the bright orange (vs. yellowish) hindwings, larger size, and lack of any transverse markings basad of the forewing subterminal line distinguish *philipiana*. The hindtibia of *G. philipiana* is also more clavate in shape than in similar species.

Description

Head - Palps black, frons and vertex pale to orange-buff; male antennae moderately bipectinate, pectinations short, 1.5 × intersegmental distance; female antennae biserrate; dorsal scales dark brown to black (males and females) or predominantly pale buff (females); eyes moderately to strongly reduced, gena exposed. ***Thorax*** - Vestiture black with pale to yellowish buff borders on vertex, patagia and tegulae; predominantly black ventrally, legs black and pale buff, tibiae pale dorsally, hind tibia distinctly clavate. ***Abdomen*** - Dorsal ground bright yellow-orange, colours more vivid in female; apex buff; medial and lateral markings black; medial markings moderately developed to slightly laterally expanded series of dots; ventral lateral spots confluent, forming black bands, segments pale bordered distally; ***Forewing*** - Male forewing length 17 mm ($n = 1$); black dorsally, vein lines complete, lines and bands yellowish buff to pale whitish buff; cubital and radial vein line often broader than other vein lines; discal cell sometimes with longitudinal pale streak; all bands except subterminal absent; subterminal and postcubital stripe complete, the latter reaching distal margin; fringe and anal margin concolourous with pale markings, costal margin entirely pale, apical portion rarely black; ventral markings similar, but dark markings with a paler yellowish cast; females with more elongate wing shape and broader pale markings. Hindwing - Ground colour bright orange, colours more saturated in female; black markings variable in extent, more reduced in females; antemedial, medial, postmedial and subterminal elements always present; antemedial elements consisting of broad basad streaks, sometimes confluent with postmedial spots resulting in predominantly black hindwing; postmedial spots large, but not confluent with reduced subterminal markings; postmedials partially or entirely broken by orange vein lines in females. *Genitalia:* not examined; the following description is based on a genitalic slide photo of *G. p. olga*; *Male:* distal portion of valve short and broad-based, rapidly tapering to bluntly pointed apex; saccular extension moderately developed, saccular process moderately developed; uncus broad-based, process relatively short and not abruptly constricted at base; juxta slightly wider than high, dorsal concavity very shallow; aedeagus relatively short and stout, vesica shorter than aedeagus.

Biology

Adult collection dates are for mid to late July. The high arctic distribution and reduced eyes indicate that *G. philipiana* is undoubtedly diurnal.

Distribution

Occurs from Wrangel Island off the coast of northeastern Siberia west to Mackenzie Delta, Northwest Territoires, and south to McKinley National Park, Alaska.

Molecular Variation

Not examined.

Remarks

Murzin (2003) and Dubatolov and Schmidt (2005) recognize *olga* as a subspecies of *G. philipiana*; it is on average darker than nominate *G. philipiana*, with the forewing lines slightly narrower and the hindwing dark markings broader and more confluent; *olga* is currently known only from Wrangel Island, while ssp. *philipiana* occurs in North America (Fig. 2-105).

GRAMMIA QUENSELI (PAYKULL)

FIGS. 2-14, 2-48, 2-80, 2-106.

Bombyx quenseli Paykull, 1793: 99.
Bombyx strigosa Fabricius, 1793: 454.
Euprepia gelida Möschler, 1849: 178
Chelonia quenseli liturata Ménétriès, 1859: 500.
Chelonia quenseli v. *falloui* Jourdheuil, 1866: 127.
Arctia gelida Schöyen, 1880: 175.

Apantesis quenseli var. *norvegica* Strand, 1919: 292.

Orodemnias quenseli daisetsuzana Matsumura, 1927: 110.

Apantesis quenseli (Paykull); Franclemont 1983: 117.

Apantesis quenseli gelida (Möschler); Franclemont 1983: 117.

Grammia quenseli zamolodchikovi Saldaitis and Ivinskis, 2000.

Grammia quenseli (Paykull); Ferguson and Opler 2006: 9.

Type Material

Bombyx quenseli: TL: "in Lapponia ad Enonteckis" [Enonteckis, Lappland, Sweden]. [type probably lost].

Bombyx strigosa: type material presumed lost.

Euprepia gelida Möschler: described from single type, sex not stated, from "Labrador" [Newfoundland, Canada]; [location of type unknown; may be in ZMHU].

Chelonia quenseli liturata: Described from one male and one female; male syntype from Kaikhan River, Lake Toko-Baikal, Yakutia, Russian Federation.

Chelonia quenseli v. falloui: TL: Simplon [Switzerland]. [location of type unkown].

Arctia gelida Schöyen: TL: Jakobselv, Sydvaranger, Norway; homonym, preoccupied by *gelida* Möschler, 1849.

Apantesis quenseli var. *norvegica*: replacement name for *gelida* Schöyen, 1880.

Orodemnias quenseli daisetsuzana: type information not available.

Grammia quenseli zamolodchikovi: type information not available.

Diagnosis

Grammia quenseli is most similar to *G. virguncula speciosa*, *G. kodara* and *G. philipiana*. Compared to these species, *quenseli* is smaller overall and has shorter male antennal pectinations, the antennae are pale-scaled not black for at least the basal third, the forewing tends to be more banded, and the hindwing is either entirely or predominantly dark grey with diffuse markings. *G. quenseli* is restricted to arctic and alpine tundra, but is sympatric with *G. philipiana* and *G. v celineata* in the western arctic, and with *G. virguncula speciosa* in Labrador. *Holarctia obliterata* is superficially similar, but lacks the dark hindwing, in addition to the significant internal genitalic differences discussed under that species.

Description

Head - Palps varying from yellowish buff to black, frons yellowish buff, vertex black centrally, yellowish buff along sides or entirely yellowish; male antennae bipectinate, pectinations relatively short, averaging 2.65 x 10^{-1} mm, (n = 6); female antennae slightly to moderately biserrate; dorsal antennal scales predominantly pale buff, rarely black; eyes strongly reduced, gena exposed at eye margins. ***Thorax*** - Vestiture black with relatively narrow, yellowish buff borders on vertex, patagia and tegulae; black ventrally, coxa and femur entirely black or black centrally, yellow at base and apex, giving striped appearance; tibia and tarsus variably pale buff and black. ***Abdomen*** - Dorsal ground colour pale buff to yellowish, reduced to lateral bands or series of spots due to very wide medial black band; lateral row of spots black; black ventrally, abdominal segments narrowly bordered pale buff distally. ***Forewing*** - Mean forewing length 12.5 mm (n = 6 males); black dorsally, vein lines complete, pale buff to yellow; postcubital line reaching distal margin; basal and antemedial band absent, or antemedial present as costal bars or below postcubital; medial band usually restricted to discal cell, sometimes nearly reaching anal margin; postmedial band variably absent, to well-developed and reaching postcubital stripe; subterminal band usually well-developed, sometimes faint; fringe and anal margin pale to yellowish buff, concolourous with remainder of line markings; costa entirely to partially pale-lined, sometimes restricted to basal 1/4; ventral markings similar, slightly more diffuse. Hindwing - Ground colour usually entirely grey with darker medial and marginal areas; ground colour occasionally pale buff to yellow with extensive black markings, especially in ssp. *gelida* and in females; ventrally, pale medial area brighter than dorsal side, lacking cast of dark grey scales. ***Male genitalia*** - Distal portion of valve gradually tapering to slightly pointed apex; extension and process of sacculus moderately developed; uncus broad-based, process evenly tapered to point, 2.5 × longer than width of base; juxta 1.75 × wider than long; aedeagus with dorsad curve at ⅔ distance beyond base; vesica with basal and medial chamber approximately equal in length and width; distal chamber small, kidney-shaped; vesica shorter than aedeagus. ***Female genitalia*** - Corpus bursae slightly pear-shaped, 2.8 × width of ostium bursa; signa rounded-triangular in shape, coarsely scobinate, relatively few spinules; posterior apophysis equal in length to papillae anales.

Biology

Adult collection dates range from mid June to late July, peaking in mid July. *Grammia quenseli* flies by day during sunny weather, males having a rapid buzzing flight typical of diurnal noctuids. Preferred habitats are dry, often rocky alpine and arctic tundra. Females very rarely fly, and are cryptically coloured on lichen-covered rocks. Larval food plants in Europe include *Lathyrus* (Fabaceae), *Taraxacum* (Compositae), *Plantago* (Plantaginaceae), *Gentiana* (Gentianaceae), and *Geum* (Rosaceae) (deFreina and Witt, 1987).

Distribution

Central European Alps (France, Switzerland, Italy, Austria, Romania) and arctic Fennoscandia (ssp. *quenseli*); eastern Siberia, west to the Amur region (ssp. *liturata*), and Hokkaido, Japan (ssp. *daisetsuzana*) (DeFreina and Witt 1987). In North America from Alaska east to Labrador, south to northern British Columbia and New Hampshire (Fig. 2-106).

Molecular Variation

Eight specimens from six locations across most of the Nearctic range of *quenseli* exhibited five haplotypes (Table 2-2). Maximum divergence within this species was 6.9%. The dramatic intraspecific sequence variation within *quenseli* is reflected by disparate occurence of *quenseli* haplotypes throughout the *Grammia* genealogy, including the Western, Eastern and Kodara lineages (Fig. 2-132). British Columbia and most Manitoba samples consisted of three closely related haplotypes of the Eastern lineage, with identical or nearly identical (one or two bp difference) *G. williamsii, G. franconia, G. f-pallida* and *G. virguncula* haplotypes. Two haplotypes, of the Western lineage, were very similar to *G. yukona*. These two species are not closely related, but both occur in the

Yukon, so this appears to represent an introgression event of *G. yukona* mtDNA into *G. quenseli*.

Remarks

This "species" surely has a long and complex biogeographical history, given its vast range over regions with a varied geological and glacial history. To treat this as a single species I believe is an oversimplification of the evolutionary divergence and variation that is undoubtedly present. However, the lack of taxonomically informative mtDNA sequence variation (Chapter 3), and the conservative morphological variation within the genus, currently does not clarify how many taxa the name *quenseli* truely encompasses.

I have not seen enough European material to comment on subspecific variation, but three palaearctic subspecies are generally recognized, *G. q. quenseli* (Scandinavia, European Alps), *liturata* (eastern Siberia and Japan) and *zamolodchikovi* (Chukotka region, Russian Federation). The eastern and north-central populations (New England, Quebec, and Labrador west to at least Darling Lake, Northwest Territories) are smaller with broader white markings than the western cordilleran taxon (Fig. 14 a,b), and are referable to subspecies *gelida* (Fig. 2-14c,d). I have not seen sufficient Palaearctic material to determine affinities of the Yukon and northern B.C. populations. DeFreina and Witt (1987) erroneously state that *gelida* was described from Vancouver Island, B.C. I have not been able to verify a record from western Montana given by Ferguson et al. (2000).

GRAMMIA MARGO SCHMIDT, NEW SPECIES

FIGS. 2-15, 2-50, 2-81, 2-107.

Grammia celia of authors, not Saunders (1863).

Type Material

Holotype **-** ♂. Canada, Alberta, Sand dunes 6 km ESE Edgerton, 1-2 June 2002, G.G. Anweiler [CNC]. ***Paratypes*** **-** 21♂♂ 14♀♀. The type series is limited to specimens from the northern Great Plains and southern Boreal region. **Alberta:** 1♂, same locality as holotype, 1 June 2004, B.C. Schmidt [BCSC]; 1♀, northwest of Opal, 10 June 1984, J.H. Acorn [UASM]; 2 ♂♂, 10 mi SE FVW [Fairview, Peace River valley], 4 May 1981, 27 May 1982, E.M. Pike [UASM]; 1♂, Nordegg, 30 May 1925, K. Bowman [UASM]; 2♂♂ 1♀, Red Deer, 15 May 1923 [UASM]; 1♂, Head of Pine Creek, [nr. Priddis], Calgary, 3 June 1903, F.H.W. Dod [CNC]; 1♂, Hot Springs Rd., Banff, 16 June 1899, N.B. Sanson [CNC]; 1♀, Enoch, 12 June 1979, E.M. Pike [UASM]; 1♀, Red Deer, 7 May 1915 [UASM]. **British Columbia:** 1♂, N side Peace River, 10V:62372N:6083E [Bear Flat], 7 June 1997, J.H. Shepard [RBCM]; 1♀, Clayhurst E[cological] R[eserve], Peace R., 10V:62258N:6855E, 24 May 1997, J.H. Shepard [RBCM]. **Northwest Territories:** 2 ♂♂, Ft. Smith, 4 June 1950, J.B. Wallis [CNC]. **Manitoba:** 9 ♂♂ 9♀♀, Aweme, various dates, N. Criddle [CNC]; 1♂, Miniota, 26 May 1937, H.A. Gibbon [CNC]; 1♂, 2 mi. W of Stockton, 20 May 1958, J.F. McAlpine [CNC].

Etymology

I am pleased to name this species after my wife Margo, who has supported and encouraged me throughout my entomological pursuits. The name is used as a noun in apposition.

Diagnosis

The overall wing pattern of *G. margo* is similar to *G. williamsii* and *G. franconia.* Compared to *G. williamsii*, *G. margo* has shorter antennal pectinations, smaller eyes, smaller and more elongate wings, the postcubital forewing band does not extend beyond the subterminal band (usually so in *G. williamsii*), never has pink hindwings, flies earlier in the spring and is strictly diurnal. The two species occur in strict sympatry at several sites in Alberta (Peace Rive canyon and Edgerton sand hills). Compared to *G. franconia, G. margo* has smaller eyes and shorter antennal pectinations, is slightly smaller overall, exhibits more dull-coloured hindwings, flies earlier in the season and is diurnal while *G.*

franconia is nocturnal. *Grammia margo* is limited to sandy, gravelly or eroding grasslands, while *G. franconia* is restricted to dry, openly wooded granite ridgetops.

Description

Head - Palps dark brown to black, frons and vertex pale buff; male antennae moderately bipectinate, pectinations averaging 3.15 × 10^{-1} mm, ($n = 6$); female antennae slightly biserrate; dorsal scales dark brown to black, often with scattered buff scales; eyes strongly reduced with gena exposed at eye margin, mean diameter 5.9 × 10^{-1} mm. ***Thorax*** - Vestiture black with pale to yellowish buff borders on vertex, patagia and tegulae; black ventrally, base of coxa and distal area usually with buff scales; coxa and femur black, tibia and tarsus pale buff dorsally, black ventrally. ***Abdomen*** - Dorsal ground colour pale yellow, pale buff near apex; medial and lateral markings black, medial line broadened; male pale buff ventrally, lateral black markings broad but not confluent at midline, female entirely black ventrally; both sexes occasionally entirely black ventrally and dorsally. ***Forewing*** - Male forewing length averaging 12.3 mm ($n = 6$ males); dark brown to black dorsally, vein lines absent; bands pale buff; medial band well developed, not extending beyond postcubital stripe, the latter not extending beyond subterminal band; postmedial band well developed, not extending beyond postcubital; subterminal band complete, angled slightly at M_3, costal section not curved; fringe and anal margin concolourous with pale markings, occasionally dark brown; basal ⅔ of costa pale-lined; ventral markings similar, but dark markings with a paler yellowish cast; sexes similar. Hindwing - Ground colour dull yellow to orange-yellow, black markings variable in extent but nearly always confluent; occasionally entirely black; similar ventrally, but dark markings with a paler yellowish cast; sexes similar. ***Male genitalia*** - Distal portion of valve gradually tapering to rounded apex; saccular extension moderately developed, saccular process moderately developed; uncus broad-based, process evenly tapered to point, 2.5 × as long as width of base; juxta 1.75 × wider than height, dorsal concavity relatively shallow; aedeagus with dorsad curve at ⅔ distance beyond base; medial chamber of vesica short, about as long as wide, minutely scobinate; distal chamber kidney-shaped, twice as long as wide, coarsely scobinate; diverticuli moderately developed. ***Female genitalia*** - Ductus bursae unsclerotized; corpus bursae slightly pear-shaped, 3 × width of ostium bursa; signa round, averaging about 2.2×10^{-1} mm, coarsely scobinate; posterior apophysis equal in length to papillae anales.

Biology

The peak flight period is in late May to early June, with collection records ranging from early May to mid June. Nearly all records for this species are from sandy or gravelly habitats, particularly prairie and parkland sand dunes. Adults are apparently strictly diurnal. The immature stages are unknown.

Distribution

Grammia margo occurs in grassland and transitional habitats of the northern Great Plains and Rocky Mountain front ranges, south to east-central Arizona (Fig. 2-107). It is rarely collected since it is diurnal and inconspicuous, and it likely occurs throughout the central and northern Great Plains. Records for Ft. Smith, Northwest Territories and the Peace River region of Alberta / B.C. represent relict grassland habitats.

Molecular Variation

Four specimens of *G. margo* from Alberta and British Columbia exhibited two haplotypes, one shared with *G. virguncula* and *parthenice*, the second with *virguncula*, *parthenice*, *elongata*, and *williamsii*, all of the Eastern lineage (Table 2-2, Fig. 2-134).

Remarks

This small, diurnal species is rarely collected, and the rapid, buzzing flight makes it easy to overlook. Most specimens in the type series were identified as *G. williamsii*, and although sympatric, the two species are relatively easy to distinguish, as noted under 'Diagnosis'. Closely related to *G. franconia,* and the two may eventually prove to be the same species; however, the structural, phenotypical and ecological differences, and the available molecular data, support the recognition of these taxa as separate species.

A single female specimen from the Yukon may be referable to this species (reported as *Grammia blakei* in Lafontaine and Wood [1997]); however, the wing markings fall outside the variation of other examined *G. margo* females and the record is well outside the range of other records, and I am therefore excluding it from the type series.

GRAMMIA FRANCONIA (H. EDWARDS), REVISED STATUS

FIGS. 2-16, 2-51, 2-82, 2-108.

Arctia franconia Hy. Edwards, 1888: 184.
Grammia celia of authors, not Saunders (1863).

Type Material

Described from a male holotype [AMNH, photograph examined] from Franconia, White Mountains, New Hampshire, USA.

Diagnosis

Most similar to *G. margo, G. williamsii* and northern populations of *G. figurata*. See 'Diagnosis' under *G. margo* for comparison to that species. Reddish-hindwing *G. franconia* could be mistaken for *G. williamsii*, but the eyes are smaller, antennal pectinations shorter and the postcubital stripe does not extend beyond the subterminal band, usually extending slightly past as a fine point in *williamsii*. Also, the forewing shape is narrower, and *G. franconia* flies earlier in the season than *G. williamsii*.The ranges of the two are currently not known to overlap, but both species could be sympatric in east-central Ontario. The northern populations of *G. figurata* (i.e. New England / Great Lakes region) can be similar to *G. franconia*, where *G. figurata* specimens can have a fully developed forewing subterminal band and a yellow or orange hindwing with heavy black markings; *G. franconia* can be separated by the smaller eye size and shorter antennal pectinations, in addition to a smaller, narrower fore- and hindwing and less robust thorax and abdomen.

Description

Head - Palps dark brown to black, rarely with buff apex; frons and vertex varying from yellowish buff to entirely brown - black; male antennae moderately bipectinate, pectinations averaging 4.24×10^{-1} mm, ($n = 6$); female antennae slightly biserrate; dorsal scales dark brown to black; eyes well developed, mean diameter 7.6×10^{-1} mm. ***Thorax*** - vestiture black dorsally with yellowish buff borders on vertex, patagia and tegulae, borders sometimes thin; ventral vestiture dark brown, yellowish laterally with yellowish central tuft, varying to entirely black; legs buff and black varying to entirely black. ***Abdomen*** - Dorsal ground colour yellow, not markedly paler near apex; entirely black in about 30% of specimens, or with medial black band very broad; yellowish buff ventrally with broad, black lateral spots, or entirely black, particularly females. ***Forewing*** - Male forewing length averaging 14.5 mm ($n = 6$ males); black dorsally, vein lines absent; bands pale buff; medial band well developed, not extending beyond postcubital stripe, the latter not extending beyond subterminal band; postmedial band well developed, not extending beyond postcubital; subterminal band complete, not angled or only slightly so at M_3, costal section not curved; fringe and anal margin usualy dark brown – black, rarely black and buff; costa dark or with pale costal line of variable extent, up to ⅔ of distance from base; ventral markings similar, but dark markings with a paler yellowish cast; sexes similar. Hindwing - Ground colour yellow, orange-yellow, or pinkish orange; black markings variable in extent but always confluent, varying to entirely black hindwing; similar ventrally, but dark markings with a paler yellowish cast; sexes similar. ***Male genitalia*** - Distal portion of valve gradually tapering to rounded apex; saccular extension moderately developed, saccular process moderately developed; uncus broad-based, process evenly tapered to point, 3 × as long as width of base; juxta 2.5 × wider than height, dorsal concavity relatively shallow; aedeagus with dorsad curve at ⅔ distance beyond base; medial chamber of vesica short, slightly wider than long, minutely scobinate; distal chamber kidney-shaped, twice as long as wide, coarsely scobinate; diverticuli well developed. ***Female genitalia*** - Ductus bursae unsclerotized; corpus bursae pear-shaped, 3 × width of ostium bursa; signa round to slightly elongate, averaging about 2.9×10^{-1} mm, coarsely scobinate; posterior apophysis equal in length to papillae anales.

Biology

Adult collection dates indicate a flight period of mid May to late June, peaking in early June. Adults of both sexes come to light, although females are rarely collected. *Grammia franconia* occurs in dry, rocky or sandy habitats, often in pine barrens. This species has a very localized distribution, although it can be fairly common in the right habitat. The immature stages are unknown.

Distribution

Examined specimens represent only a few localities in Ontario, Wisconsin, Quebec and Nova Scotia (Fig. 2-108), but this species is likely more widespread in northeastern North America. Many of the literature records and museum specimens are mixed in with the northern form of *G. figurata*.

Molecular Variation

Six specimens of *G. franconia* from two localities showed three haplotypes in the Eastern lineage, differing by one or two base pairs (Fig. 2-134, Table 2-2). Two haplotypes were shared among multiple species; one with *G. virguncula, G. williamsii* and *G. quenseli* (EA11; Fig. 2-134), and another with *G. williamsii* (EA24; Fig. 2-134). The third haplotype was unique to *G. franconia* (EA23; Fig. 2-134).

Remarks

This species appears to be most closely related to *G. margo*. The structural, behavioural and ecological differences discussed under 'Diagnosis', and the lack of clinal variation in these characters between the easternmost populations of *G. margo* (Manitoba) compared to Ontario *G. franconia*, lead me to conclude that the two are distinct species.

GRAMMIA FIGURATA (DRURY)

FIGS. 2-17, 2-52, 2-83, 2-109.

Bombyx figurata Drury, 1773: pl. 12, f. 4

Euplagia ceramica Hübner, [1820]: 180.

Arctia celia Saunders, 1863: 59. **New Synonomy.**

Arctia snowi Grote, 1875: 197.

Arctia excelsa Neumögen, 1883a: 70.

Arctia phyllira ab. *lugubris* Hulst, [1887]: 182.

Apantesis figurata var. *preciosa* Nixon, 1911: 232.

Apantesis figurata (Drury); Franclemont 1983: 117.

Grammia figurata (Drury); Ferguson and Opler 2006: 11.

Type Material

Bombyx figurata: described from an unstated number of specimens, although a female is illustrated; the type material is lost; the type locality is Virginia, [USA].

Euplagia ceramica: location of type material not known.

Arctia celia: described based on a male specimen from Toronto, Ontario, [Canada] [CNC, examined]. The holotype is typical of the northern populations of *figurata*, which exhibit yellow hindwings and often have the subterminal forewing band well developed. The name *celia* has been variously applied to northern *G. figurata* and *G. franconia* n. sp., but the *celia* holotype is clearly the same species as the northern *figurata* forms.

Arctia snowi: The female type specimen is in the USNM (type # 33673) [not examined]. Type locality: Kansas, [USA].

Arctia excelsa: male holotype from North Carolina in USNM (Smith 1938a) [not examined].

Arctia phyllira ab. *lugubris*: this name was proposed to describe a variant with entirely black hindwings, and is therefore an unavailable infrasubspecific name.

Apantesis figurata var. *preciosa*: this name was proposed to describe a form of *figurata* with yellow hindwings, and is therefore an unavailable infrasubspecific name.

Diagnosis

Most specimens of *G. figurata* can easily be recognized by absence or reduction of the forewing subterminal band, and the fusion of the hindwing postmedial and subterminal spots into one relatively even-bordered marginal band. In the southeastern Great Plains where the range of *G. figurata* overlaps with *G. f-pallida*, *G. figurata* can be separated with the characters given under *G. f-pallida*. Some variants of *G. figurata* from northern populations (Great lakes / New England) can be similar to *G. franconia* and *G. williamsii*, see Diagnosis under those species.

Description

Head - Palps black, frons and vertex pale to pinkish buff; male antennae moderately bipectinate, pectinations averaging 5.10 x 10^{-1} mm, (n = 9); female antennae slightly biserrate; dorsal scales dark brown to black; eyes well developed, mean diameter 1.04 mm (n = 9). ***Thorax*** - Vestiture black with pale to yellowish buff borders on vertex, patagia and tegulae; black ventrally, base of coxa with yellowish buff scales; coxa and femur black, tibia and tarsus variable, pale buff dorsally, black ventrally, or entirely black. ***Abdomen*** - Dorsal ground colour yellow, orange or pink, slightly paler near apex, or entirely black, particularly females; medial and lateral markings black; pale buff ventrally with variable lateral black markings, or entirely black. ***Forewing*** - Male forewing length averaging 15.77 mm (n = 6 males); dark brown to black dorsally, vein lines absent; bands pale buff to ivory; medial band usually well developed, not extending beyond postcubital stripe; postcubital variable in length, extending only to postmedial or slightly past subterminal; medial band well developed, with slight angle at M_3 or straight; subterminal band absent to well developed; fringe and anal margin varying from pale buff to dark brown and combinations thereof; costa dark or variably pale-lined, up to ⅔ of the distance from base; ventral markings similar, but slightly paler and with distinct yellowish cast; wing shape in females slightly more elongate, but otherwise similar. Hindwing - Ground colour highly variable, ranging from yellow to scarlet and vivid pink; black markings variable in extent but postmedial and subterminal elements nearly always confluent to form a broad marginal band; medial spot usually prominent, antemedial spots varying from well developed and streaked basad, to absent; hindwing occasionally entirely black, or with very restricted coloured medial area; similar ventrally, but dark markings with a paler yellowish cast; sexes similar. ***Male genitalia*** - Distal portion of valve gradually tapering to rounded apex; saccular extension reduced, saccular process moderately developed; uncus broad-based, process evenly tapered to point, 2.5 × as long as width of base; juxta 2 × wider than height; aedeagus with dorsad curve at ⅔ distance beyond base; medial chamber of vesica slightly longer than wide, minutely scobinate; distal chamber kidney-shaped, twice as long as wide, coarsely scobinate; diverticuli moderately developed. ***Female genitalia*** - Ductus bursae unsclerotized; corpus bursae pear-shaped, 3.3 × width of ostium bursa; signa round, realtively small, averaging 2.2×10^{-1} mm, coarsely scobinate; posterior apophysis slightly longer than papillae anales.

Biology

Grammia figurata is bivoltine in northern Ohio (Rings and Metzler 2002), but most records from the northern part of the range are for May through June. In the southwest (Kansas, Oklahoma, Texas), records range from April to October, undoubtedly representing more than one yearly generation.

Distribution

Southern Ontario and New Hampshire south to Georgia, west to Colorado and Texas (Fig. 2-109). Reports of this species from Quebec (Handfield 1999) are likely referable to *G. franconia.*

Molecular Variation

Ten specimens from six localities exhibited six haplotypes, with a mean and maximum intraspecific divergence of 0.49% and 1.52%, respectively (Table 2-2). With the exception of one Colorado specimen (FI2; Fig. 2-134), *G. figurata* formed a lineage (FI3:FI7; Fig. 2-134) which included three of four *G. f-pallida* haplotypes, and two eastern North American *G. virguncula* haplotypes (Fig. 2-134).

Remarks

This taxon displays remarkable phenotypic variation across its range, but there are no reliable data to suggest that more than one species is involved. The northern forms of *G. figurata* (Fig. 2-17b,c), with yellow or often melanic hindwings, and well-developed forewing subterminal bands, differ considerably from the pink hindwing/unbanded forewing forms (east-central and southern U.S.), yet many populations (e.g. southern Ontario) display individual variation to the point where no two specimens are exactly alike. This has resulted in the long-standing misapplication of the name *celia*, as discussed above under 'Type Material' and *Grammia franconia*.

The taxonomic status of some Colorado populations is not yet fully resolved, but I am retaining them as *G. figurata* until more data becomes available; this pertains to the slightly larger taxon with a fully developed subterminal forewing band and hindwings with more discrete rather than banded markings (Morgan, Douglas and Arapahoe Counties, CO); females resemble males in this taxon (A. Warren, pers. comm.), suggesting it is closely related to or conspecific with *G. figurata*, not *G. f-pallida*.

GRAMMIA F-PALLIDA (STRECKER)

FIGS. 2-18, 2-53, 2-84, 2-110.

Arctia f-pallida Strecker, 1878; Ann. Rep. Chief of Engineers, App. SS: 1860

Arctia quadranotata Strecker, 1878; Proc. Davenport Acad. Nat. Sci, 2: 271, pl. 9, f. 6 [**Note:** published in October 1878, after the June-July issue in which the description of *f-pallida* Strecker 1878 appeared (Smith 1938a)]

Apantesis sociata Barnes and McDunnough, 1910: 149.

Apantesis moierra Dyar, 1914: 161.

Apantesis f-pallida (Strecker); Franclemont 1983: 117.

Apantesis quadranotata (Strecker); Franclemont 1983: 117.

Apantesis sociata (Barnes and McDunnough); Franclemont 1983: 117.

Grammia f-pallida (Strecker); Ferguson and Opler 2006: 11.

Type Material

Arctia f-pallida: male holotype from Rio Navajo, [Archuleta Co.,] Colo[rado], [USA], in FMNH according to Smith (1938a) [not examined], but this specimen is currently not in the FMNH numbered colour slides of type specimens, and there are no types missing judging by the complete numbering sequence of slides. It therefore appears that the *f-pallida* type has been missing for some time.

Arctia quadranotata: described from "several examples" from Texas according to the original description, although Strecker (1899) subsequently lists a single female as the type material. The female syntype labeled "Dallas/ Tex. Boll", "orig. type.", "Arctia Quadranotata/ Streck/ Dallas, Texas./ orig. Type, J. Boll", "Arctiidae/ genitalia slide/ No. 1096", Lepidoptera Type/ Photograph No. 197/ Field Museum", "Lectotype ♀/ det. A. Watson 1966", "CNC/ colour slide/ 662212", "LECTOTYPE/ *Arctia/ quadranotata* Strecker/ B.C. Schmidt 2007" is hereby designated as **lectotype** to ensure the stability of this name [FMNH, photograph examined].

Apantesis sociata: female holotype from Fort Wingate, New Mex[ico, USA] [USNM, examined].

Apantesis moierra: female holotype from Dallas, Texas, [USA], USNM type # 19075 [USNM, not examined].

Diagnosis

The reduced forewing banding pattern, with complete or nearly complete absence of the w-shaped forewing subterminal band is characteristic of only *G. f-pallida* and most *G. figurata*. Compared to *G. figurata, G. f-pallida* is generally smaller (forewing length < 34mm vs. > 34mm), and the sexes have a dimorphic forewing pattern in *G. f-pallida* (female *G. f-pallida* always have nearly or entirely dark forewings), while female *G. figurata* exhibit a pattern similar to that of males. Although the differences in wingspan between *G. f-pallida* and *G. figurata* can be subtle, the difference in body size is more marked, reflected by the smaller eye diameter in *G. f-pallida*, which is less than 0.90 mm (mean 0.81 mm), greater than .90 mm (mean 1.04 mm) in *G. figurata*. *Grammia f-pallida* and *G. figurata* remain distinct where the ranges overlap in the southeastern Great Plains;

the two species are sympatric and synchronic at Fort Supply, Oklahoma, flying together in late August.

Description

Head - Palps black; frons and vertex pale to reddish buff, or black and buff laterally; male antennae moderately bipectinate, pectinations averaging 4.43×10^{-1} mm, ($n = 6$); dorsal scales dark brown to black; eyes well developed, mean diameter 8.14×10^{-1} mm ($n = 6$). ***Thorax*** - Vestiture black with pale to yellowish buff borders on vertex, patagia and tegulae; females usually entirely dark brown - black; dark brown to black ventrally, base of coxa with pinkish buff scales; coxa and femur black, tibia and tarsus variable, pale buff dorsally, black ventrally, or entirely black. ***Abdomen*** - Dorsal ground colour pink, not noticeably paler near apex; medial and lateral markings dark brown to black; entirely black ventrally. ***Forewing*** - Male forewing length averaging 13.9 mm (n = 6 males); dark brown to black dorsally, vein lines absent; bands pale buff to ivory; medial and postmedial band and postcubital stripe well developed in males; subterminal band absent, or reduced to slight v-shaped bar at M_3; antemedial band sometimes expressed as costal bar; fringe, anal margin and costa dark brown, anal margin rarely pale at base; forewing entirely dark brown in females, or with bands reduced to one or two bars or spots in discal cell; ventral markings similar, but slightly paler and with yellowish cast; wing shape in females slightly more elongate, but otherwise similar. Hindwing - Ground colour pinkish red, rarely yellow (Colorado); black markings restricted to broad, relatively smooth-bordered margin consisting of merged postmedial and subterminal elements; medial discal spot prominent, antemedial spots usually absent, sometimes present and streaked basad; similar ventrally, but dark markings with a paler yellowish cast; sexes similar. ***Male genitalia*** - Distal portion of valve gradually tapering to rounded, slightly pointed apex; saccular extension reduced, saccular process moderately developed; uncus broad-based, process evenly tapered to point, 2x as long as width of base; juxta 2 × wider than height; aedeagus with dorsad curve at ⅔ distance beyond base; medial chamber of vesica slightly longer than wide, minutely scobinate; distal chamber kidney-shaped, twice as long as wide, coarsely scobinate; diverticuli well developed. ***Female genitalia*** - Ductus bursae unsclerotized; corpus bursae pear-shaped, 3 × width of ostium bursa; signa round, relatively large, averaging 3.0 × 10^{-1} mm, coarsely scobinate; posterior apophysis equal in length to papillae anales.

Biology

Collection dates for adults indicate that *G. f-pallida* is bivoltine in at least parts of its range, with dates from the Davis Mountains in western Texas ranging from late April to early May and July through August. Southeastern Colorado / western Oklahoma records are for late August, and New Mexico and Utah for June / July and late August. In central Colorado it flies in June and July. The early stages are undescribed.

Distribution

Distributed from southeastern Utah and Colorado south through eastern Arizona, New Mexico, and eastern Texas (Fig. 2-110). Ferguson *et al.* (2000) also give a record for west-central Nevada, and it almost certainly occurs in Mexico, although I have seen no specimens from there.

Molecular Variation

Grammia f-pallida samples consisted of two specimens from two localities (CO, OK) with a single haplotype of the Eastern lineage (Table 2-2, Fig. 2-134). This haploptye differed by only two base pairs from a a haplotype shared by *G. virguncula* and *G. figurata* (Fig. 2-134).

GRAMMIA INCORRUPTA (HY. EDWARDS)

FIGS. 2-19, 2-54, 2-85, 2-111.

Arctia incorrupta Hy. Edwards, 1881; Papilio 1: 38
Arctia ochracea Neumögen 1883b; Papilio 3: 151 (preocc. by Stretch, 1872)
Arctia nevadensis var. *sulphurica* Neumögen, 1885; Entom. Amer. 1: 93
Apantesis geneura incorrupta (Hy. Edwards); Franclemont 1983: 117.
Grammia nevadensis complex [in part] Ferguson *et al.* 2000: 48, 130.

Grammia incorrupta (Hy. Edwards); Ferguson and Opler 2006: 11, Ferguson and Schmidt 2007: 42.

Type Material

Arctia incorrupta: A lectotype for *Arctia incorrupta* was designated by Ferguson and Opler (2006), but no details pertaining to the specimen are provided, other than the fact that it was collected at Prescott, Arizona (as were three of the original syntypes, according to the description). All specimens from Prescott were examined among Ferguson's material at the USNM, and no specimen bears any label indicating that Ferguson had intended it as the lectotype. According to the original description, *Arctia incorrupta* was based on three female specimens from Prescott, Arizona and one male from [The] Dalles, Oregon (Edwards, 1881). According to Smith (1938a), there were three *incorrupta* specimens from the Edwards collection in the AMNH at the time, two males from "Arizona" and one male from "[The] Dalles, Ore[gon]." As noted by Smith (1938a), Edwards likely either mistook the Arizona males as females, or the mix-up was the result of a typographical error. At any rate, all evidence suggests that the two Edwards specimens remaining at the AMNH are syntypes, one from "Oregon" with a "No. 8130 Coll. Hy. Edwards" label, the second from Prescott, Arizona with a "No. 8128, Coll. Hy. Edwards" label (S. Rab-Green, pers. comm., 2005). Since the Oregon specimen is in all likelihood referable to *Grammia nevadensis superba* (*incorrupta* is not known to occur in OR), I designate the Arizona specimen as **lectotype**, bearing the labels: "Prescott, Arizona", "No. 8128 / Collection Hy. Edwards", "Arctiidae/ genitalia slide No. 1262", "Lectotype by A. Watson 1967", "LECTOTYPE/ *Arctia*/ *incorrupta* H. Edwards/ B.C. Schmidt 2007".

Arctia ochraecea: Unavailable primary homonym of *ochracea* Stretch 1872. The holotype is the same specimen subsequently designated as the holotype of *sulphurica* (see below) according to Neumögen (1883b), although the specimen no longer bears any labels indicating that it is the type of *ochraecea* Neumögen.

Arctia nevadensis var. *sulphurica*: proposed as a replacement name for *ochracea* Neumögen 1883, a homonym of *ochracea* Stretch 1872 (a junior subjective synonym of *Grammia ornata*). The holotype of *sulphurica* in the USNM bears the labels "Arctia/ nevadensis / v. sulphurica. / Type. Neumgn.", "TYPICUM/ SPECIMEN", "Prescott/ Arizona.", "Col./ B. Neumögen.", "Type No./ 33679/ U.S.N.M.", "♂ genit. on/ slide/ Sept. 6, 1931/ MES 1536". *Sulphurica* is an unavailable infrasubspecific name, based on a colour variant.

Diagnosis

Due to the significant phenotypic variation in *G. nevadensis*, *G. incorrupta* was long confused with this species. Most of this confusion stems from the similarity of *G. n. geneura* with *incorrupta*, as both taxa are relatively large, broad-winged and brightly coloured. Most specimens of *G. incorrupta* can be distinguished from *G. nevadensis* by the longer antennal pectinations, broader forewing shape, reduced hindwing markings, and the larger signa of the female bursa. Males very rarely express the all-dark thorax phenotype (I have seen only three specimens like this) common in *G. n. nevadensis* and *G. n. superba*, and the entirely pale thoracic collar (patagia) seen in about ¼ of *G. incorrupta* specimens does not occur in any *nevadensis* populations. *Grammia incorrupta* is multivoltine, while *G. nevandensis* has a single yearly flight. I have not been able to find consistent differences in the male genitalia. A comparison of characters is given in Table 2-3.

Description

Head - Frons, vertex and palps with dark brown to black vestiture, frons and vertex varying from dark with buff borders to (rarely) entirely pale buff; eye fully developed, mean maximum diameter = 1.07 mm (n = 6); male antenna strongly bipectinate, longest branches averaging 7.55×10^{-1} mm, or 4.31 times intersegmental distance (n = 12; AZ, NM, CO); female antenna slightly to moderately biserrate; antenna dark-scaled in both sexes, occasionally with pale buff scales along vertex of shaft and pectinations. ***Thorax*** - Patagia, tegula and vertex of thorax usually dark-brown to black bordered with pale buff, patagia entirely pale buff in about 25% of specimens; yellow ventrally, legs dark brown with variable amounts of pale buff. ***Abdomen*** - Ground colour orange-pink, rarely yellow-orange, anal tuft pale buff; medial spots wider in females, particularly on last two segments; yellowish-buff to pale buff ventrally, dark brown to black markings consisting of two rows of spots, bordered distally at each segment margin by pale buff; females usually entirely or predominantly dark brown–black ventrally. ***Forewing*** - Mean forewing length = 18.6 mm (n = 9); usually with complete set of transverse bands, as in *G. nevadensis,* basal and antemedial bands rarely reduced or absent; bands pale buff to yellowish buff, rarely pinkish buff; fringes concolorous with bands, lacking dark scales; anal dash absent. female forewing bands more yellowish than males. Hindwing - Ground colour pink to yellowish pink, very rarely yellow; markings most often restricted to three postmedial spots and traces of subterminal spots at margin, but never confluent; antemedial and medial spots generally absent or reduced, more prevalent in females; females with more vivid, brighter hindwing pink; ventral pattern similar, but colours less vivid. ***Male genitalia*** - Distal portion of valve varying from broad to slender, but not constricted near middle, and apex rounded; saccular extension reduced to moderately developed; uncus broad-based, process evenly tapered to point; juxta wider than long; aedeagus with dorsad curve at ⅖ distance beyond base; distal chamber of vesica kidney-shaped, scobinate. ***Female genitalia*** - Ductus bursae unsclerotized; corpus bursae with three round and one oval signa, roughly equal in size; appendix bursae with angled elbow, not evenly coiled, finely but conspicuously scobinate; posterior apophysis about 1.5 × longer than length of papillae anales.

Biology

This species has two flights annually, with adult collection dates ranging from late April to early October. The peak of each flight varies according to local climate and seasonal rains (Singer 2000), peaking in June and October in southeastern Arizona (Singer 2000). *Grammia incorrupta* inhabits arid grasslands and open woodlands associated with the mountain ranges of the southwestern US and Mexico. Unlike species of the *nevadensis* group, females of *incorrupta* come to light.

Larvae feed on a large variety of primarily herbaceous, flowering plants, belonging to at least 80 species in 50 families (Singer 2000). Larvae parasitized by tachinid flies are able to "self-medicate", increasing their uptake of toxic plants in response to parasitism (Bernays and Singer 2005).

Distribution

Grammia incorrupta occurs from southern Colorado and southeast Kansas south through Arizona, New Mexico and western Texas into Mexico (states of Aguascalientes and Nuevo Leon), and west to southeastern California (Fig. 2-111).

Molecular Variation

Four specimens of *G. incorrupta* from four localities (TX, AZ, NM, CO) all exhibited unique haploptypes, with a maximum intraspecific divergence of 2.3 % (Table 2-2). *Grammia incorrupta* haplotypes were monophyletic (Incorrupta lineage, Fig. 2-132), forming a well-supported clade consisting of *G. incorrupta, G. allectans* and *G. ursina* haplotypes (Fig. 2-136). Haploptypes of *G. incorrupta* were at least 3% divergent from *G. ursina* (Table 2-2, Fig. 2-132).

Remarks

I have not seen specimens of *incorrupta* and *nevadensis* from the same site, although the ranges of the two should overlap in southern Colorado, southern Utah and possibly southern Nevada. *Grammia incorrupta* and *G. bowmani* fly together at Colorado National Monument, Mesa County, Colorado. The black thorax form is very rare in *incorrupta* (Fig. 2-19b), and I have seen it only from Yavapai County, Arizona and McGaffey, New Mexico.

GRAMMIA ALLECTANS FERGUSON

FIGS. 2-20, 2-55, 2-112.

Grammia allectans Ferguson, 1985: 231, figs. 55-58, 119-122.
Grammia allectans Ferguson; Ferguson and Opler 2006: 11.

Type Material

Male holotype from 10 mi. W of El Salto, 9,000', Durango, Mexico. [CNC, examined]; One female and 16 male paratypes [CNC, USNM, AMNH, LACM].

Diagnosis

Grammia allectans is somewhat similar to *G. williamsii*, but can be distinguished from that species by the longer antennal pectinations, presence of a forewing basal, medial (and often antemedial) band. Also, the postmedial band is strongly curved basally near the costa, not straight or nearly so as in *G. williamsii*, and the male vesica is more kidney-shaped than globose. The ranges of these two species do not overlap, with *G. allectans* occuring to the south of *G. williamsii* in southern Arizona and Mexico.

Description

Head - Frons, vertex and palps yellowish buff, frons and palps dark brown laterally; male eyes fully developed, mean maximum diameter = 7.88×10^{-1} mm (n = 3; AZ, MEX), but averaging larger in the AZ populations according to Ferguson (1985); female eyes ½ the size of male eyes [not examined; Ferguson 1985]; male antennae strongly bipectinate, pectinations averaging 6.50×10^{-1} mm, 4.13 times longer than intersegmental distance (n = 3); dark brown and buff dorsal scales; female antennae bipectinate, branches 1.5 times intersegmental distance [not examined; Ferguson 1985]. ***Thorax*** - Vestiture of thorax dark brown to black, patagia, tegula and vertex bordered with yellowish buff; underside yellowish buff, legs predominantly pale buff. ***Abdomen*** - Ground colour pinkish-buff, pale buff near apex; medial and lateral markings dark brown to black; pale buff ventrally, dark brown to black markings consisting of two rows of spots, bordered distally at each segment margin by pale buff. ***Forewing*** - Mean forewing length 14 mm (n = 3 males); ground colour dark brown, fringe yellow-buff or dark brown; banding pattern buff to yellowish; relatively complete banding pattern; postcubital, basal, medial, postmedial and subterminal band well developed but thinner than in *G. nevadensis* group, antemedial band present or absent; anal dash absent; female similar, bands slightly broader. Hindwing - Ground colour orange-red, patterned with dark brown; antemedial markings well developed, often confluent and extending basally and along anal margin; medial spot distinct; postmedial and subterminal markings usually one broad marginal band with irregular proximal border; female with dark markings less developed, not confluent; underside similar but paler in colour. ***Male genitalia*** - Distal portion of valve broad, gradually tapering to rounded apex; saccular extension reduced, saccular process moderately developed; uncus broad-based, process evenly tapered to point or with slight constriction near basal 1/3; juxta wider than long; aedeagus with dorsad curve at ⅔ distance beyond base; distal chamber of vesica broadly kidney-shaped, scobinate. ***Female genitalia*** - Not examined.

Biology

Adult collection dates range from early May to late June, with most records from mid to late June. The habitat where known is open montane pine forest.

Distribution

Known from the Chiricahua Mountains of Arizona, and the states of Durango and Sonora, Mexico (Fig. 2-112).

Molecular Variation

The single sequenced specimen exhibited a haplotype most similar to *G. incorrupta* + *G. ursina*, forming the *allectans* + *(incorrupta* + *ursina)* clade (Fig. 2-99).

Remarks

Ferguson (1985) states that the male valve is broader than in members of the *Grammia nevadensis* species group, but this character is quite variable even within *G. nevadensis,* and does not reliably differentiate *G. allectans*.

GRAMMIA URSINA SCHMIDT, NEW SPECIES

FIGS. 2-21, 2-56, 2-86, 2-113.

Arctia nevadensis Grote and Robinson; Coquillett 1898: 250.
Apantesis nevadensis (Grote and Robinson); Medlar 1940: 118, pl. 23.
Grammia nevadensis complex [in part]; Ferguson *et al.* 2000: 48.

Type Material

Holotype - male: USA: California, San Diego Co., MCAS Miramar, 20 September 1998, N. Bloomfield. ***Paratypes*** - 15 males, 2 females. **California: San Diego Co.:**, NAS Miramar 6, 30 September 1997, N. Bloomfield (1 male, EME); NAS Miramar 3, 5 October 1997, N. Bloomfield (1 male, EME); MCAS Miramar 2, 3 December 1997, N. Bloomfield (1 male, EME); MCAS Sycamore Canyon, 5 December 1997, N. Bloomfield (1 male, EME); **Riverside Co.**: Lake Matthews, 7 October 1975, J.W. Johnson (1 male, EME); same locality as previous, 19 October 1975 (1 female, EME); Gavilan Hills, 19 March 1986, F. Sala (1 female, EME); samle locality as previous, 4 October 1983 (1 male, BCSC). **Orange Co.:** Dana Point, 29 September 1936 (1 male, CNC); same locality as previous 2 October 1936 (1 male, CNC); **Los Angeles Co.:** San Clemente Island, 1 mi S navy base, 27 September 2002, Powell and DeBenedictis (1 male, EME); San Clemente Island, 2 mi S navy base, 27 September 2002, Powell and DeBenedictis (3 males, EME); San Clemente Island, mouth of Box Canyon 15 March 1986, T. Scott (1 male, EME); **Santa Barbara Co.:** Santa Rosa Island, Windmill Canyon, 25 September 2000, J. Powell (1male, EME); San Miguel Island, Nidever Canyon, 350-400 ft., 13-16 September 1995, J.A. Powell and I. Williams (1male, EME).

Etymology

The name *ursina* is derived from Latin meaning "little bear", in reference to the dense, often dark brown thoracic vestiture of this species.

Diagnosis

The wing pattern is similar to that of *Grammia nevadensis nevadensis*, from which *G. ursina* can easily be distinguished by the remarkably long male antennal pectinations (> 0.75 mm vs. < 0.75 mm in *nevadensis*), stubbier, broader forewing shape and the pale anal dash on the forewing (very rare in *G. n. nevadensis*); internally, the small corpus bursae and reduced signa 3 and 4 of the female are distinctive; the distal chamber of the male vesica are more sausage-shaped than kidney shaped. The ranges of these two taxa are not known to overlap, with *G. ursina* occuring in southwestern California, including the Channel Islands.

Description

Head - Frons, vertex and palps dark brown (vertex and frons pale buff in one specimen); eyes fully developed; male antennae strongly bipectinate, pectinations averaging 7.91 × 10^{-1} mm, 4.56 times longer than intersegmental distance ($n = 6$); antenna with predominantly dark brown dorsal scales, scattered buff scales; female antennae slighty bipectinate. ***Thorax*** - Vestiture entirely dark brown to black, or with traces of slightly lighter brown borders at margins of patagia and tegula; pale-buff borders typical of the genus seen in only one of 14 specimens; entirely dark brown ventrally, or dark brown with yellowish central tuft; legs entirely dark brown or dark brown and yellowish buff. ***Abdomen*** - Ground colour pinkish-orange, pale buff near apex; medial and lateral markings dark brown to black; pale buff ventrally, dark brown to black markings consisting of two rows of spots, bordered distally at each segment margin by pale buff; females entirely black ventrally and on dorsum of last two abdominal segments. ***Forewing*** - Mean forewing length 15.3 mm for males ($n = 9$), females 16.7 mm ($n = 2$); ground colour dark brown, fringe yellow-buff to pale buff; banding pattern usually complete as in *G. incorrupta* and *G. nevadensis*, but thinner, especially in San Clemente Island specimens; bands buff to yellowish-buff; anal dash usually present; female markings similar to male, but with band colour more yellow, forewing shape slightly more elongate. Hindwing - Ground colour pale pink to orange-pink, patterned with black; antemedial and medial markings usually absent or reduced; postmedial spots well developed; subterminal markings consisting of two to three marginal wedge-shaped spots; postmedial and subterminal markings not confluent; sexes similar, with ground colour in females a richer orange-pink; vantral pattern similar to dorsum, with less intense colours. ***Male genitalia*** - Distal portion of valve relatively narrow, gradually tapering to rounded apex; saccular extension moderately developed ventro-caudal bulge, saccular process moderately developed; uncus broad-based, process evenly tapered to point; juxta wider than long; aedeagus with dorsad curve at ⅗ distance beyond base; distal chamber of vesica broadly kidney-shaped, scobinate, spinules relatively large as in *G. incorrupta*. ***Female genitalia*** - Ductus bursae unsclerotized; corpus bursae more or less globose and relatively small, 2-2.5 × width of ostium bursa; signa 1 and 2 round to slightly elliptical, well developed, signa 3 and 4 reduced; appendix bursae with angled elbow, not evenly coiled; posterior apophysis 1.5 × longer than length of papillae anales.

Biology

Most adult collection dates range from mid September to early October, with a few extreme records from mid August to early February. The flight dates likely represent a single generation, with some variation likely due to annual and regional rainfall and temperature differences. Coquillett (1898) reared about a dozen larvae to adults of the black thorax form, from Santa Monica, CA; the larvae, almost certainly referable to this species, were described as follows: head black with sutures, lateral and ventral margin of clypeus, and dot at base of antennae yellow; integument black with purplish tinge, lighter grey below spiracles; dorsal line dull white, broken; tubercles light grey; setae black mixed with reddish to yellowish setae, the latter more numerous along dorsum and below spiracles; spiracles yellowish brown ringed with black.

Distribution

Known from the Channel Islands off the coast of southern California, although I have not seen it from San Nicholas and Santa Catalina Island; mainland southwestern California from Kern County south to San Diego County (Fig. 2-113), although it likely also occurs in adjacent parts of Baja California. The record for Monterey County, mapped by Ferguson *et al.* (2000) may also be referable to this species.

Molecular Variation

Two samples of *G. ursina* from San Clemente Island, CA exhibited two similar haplotypes, forming the Ursina lineage, which was well supported as the sister group to the Incorrupta lineage (Fig. 2-99). Minimum divergence between *G. ursina* and *G. incorrupta* lineage was 3% (Table 2-2).

Remarks

Although similar to *Grammia nevadensis* at first glance, the long antennal pectinations, broader forewing shape, and mtDNA haplotypes show that *ursina* is more closely related to *G. incorrupta* and *G. allectans*.

GRAMMIA NEVADENSIS (GROTE AND ROBINSON)

FIGS. 2-22, 2-57, 2-87, 2-114.

Arctia nevadensis Grote and Robinson, 1866: 1, pl. 1.
Arctia superba Stretch, 1873 [1874]: 227, pl. 9, fig. 12.
Arctia geneura Strecker, 1880: 270, pl. 9, fig. 5.
Apantesis gibsoni McDunnough, 1937: 152.
Callarctia nevadensis form *alexanderi* Smith, 1938b: 10.
Apantesis nevadensis (Grote and Robinson); Franclemont 1983: 117.
Apantesis geneura superba (Stretch); Franclemont, 1983: 117.
Grammia nevadensis (Grote and Robinson); Grimble *et al.* 1992: 92.
Grammia nevadensis complex [in part] Ferguson *et al.* 2000: 48, 130.
Grammia nevadensis (Grote and Robinson); Ferguson and Opler 2006: 11; Ferguson and Schmidt 2007: 40.
Grammia nevadensis geneura (Strecker); Ferguson and Opler 2006: 11; Ferguson and Schmidt 2007: 42.
Grammia nevadensis superba (Stretch); Ferguson and Opler 2006: 11; Ferguson and Schmidt 2007: 41.
Grammia nevadensis gibsoni (McDunnough); Ferguson and Opler 2006: 11; Ferguson and Schmidt 2007: 42.

Type Material

Arctia nevadensis: described from one male specimen from "Nevada" [USA], type no. 7687 in the ANSP [not examined].

Arctia superba: described from one male specimen from "Vancouver Island", [British Columbia, Canada]. The holotype male is a dissected specimen in fair condition, with missing antennae. [AMNH, photograph examined].

Arctia geneura: described from one male specimen from "Gilpin Co., Col. 8500 ft." [Colorado, USA]. The holotype [FMNH, photograph examined] bears the labels "Arctia Geneura / Gilpin Co., Col. Streck / 8500 ft. / Orig. Type. G.H.French", "A. Geneura / Streck / Gilpin Co. Col. / orig. G.H.French / Type", "orig. / type.", "Arctiidae / genitalia slide / No. 1222", "HOLOTYPE [male] / det. A.Watson 1966", "Lepidoptera Type / Photograph No. 195 / Field Museum".

Apantesis gibsoni: the holotype male is in the CNC [examined], bearing the labels: "Calgary [Alberta, Canada] / 7 Aug. 1902 / in light globe / T.N.Willing.", "HoloTYPE / Apantesis / gibsoni McD / No 4209". The specimen is in good condition, except that the abdomen is missing. McDunnough (1937) designated a female allotype from Arcola, SK (misspelled as "Areola"), and a series of 23 male and three female paratypes, from Aweme, MB, Rounthwaite, MB and Calgary, AB.

Callarctia nevadensis form *alexanderi*: male holotype in USNM according to OD (Smith 1938b). An unavailable infrasubspecific name proposed for the dark thorax form.

Diagnosis

This species is widespread throughout western North America, and can be the most common *Grammia* species in some areas. The large amount of geographic variation can make this a difficult species to recognize, but the complete lack of forewing vein lines, complete or nearly complete complement of forewing bands, and single flight late in the season (late summer/early fall) are good diagnostic characters. It is most similar to *G. incorrupta, G. ursina,* and *G. bowmani*, and diagnostic characters are given in each of the species accounts, in addition to those given for differences between *G. nevadensis/incorrupta* in Table 2-3. See also 'Remarks' below.

Description

Head - Frons, vertex and palps with dark brown vestiture, varying to dark brown with pale buff scales on frons, apex of palps and lateral borders on vertex. Male antennae strongly bipectinate, anterior and posterior pectinations nearly equal in length (anterior : posterior = 0.97 : 1), posterior pectinations averaging 6.00×10^{-1} mm, 3.85 times longer than intersegmental distance (*n* = 31; AB, SK, NV, CA, YT). Female antennae strongly biserrate to slightly bipectinate. Antennal scales dark brown, with varying amounts of pale buff scales dorsally along shaft and pectinations. ***Thorax*** - Vestiture of thorax, including patagia and tegula, entirely dark brown to black, or bordered with pale buff; yellow to pale buff ventrally. Leg scales entirely dark brown varying to predominantly pale buff. ***Abdomen*** - Ground colour generally orange-pink, varying to pale yellow and pale buff, particularly near apex; medial and lateral markings dark brown to black, sometimes confluent but usually bordered distally by ground colour. Yellowish-buff to pale buff ventrally, dark brown to black markings consisting of two rows of spots, bordered distally at each segment margin by pale buff. ***Forewing*** - Ground colour dark brown to black, fringe white to pale buff, rarely with dark brown scales; forewing bands white to pale buff, rarely pink-buff; basal and antemedial band variably developed, present as at least a pale spot at costa; medial, postmedial and subterminal band well developed and nearly always present; antemedial, medial and postmedial bands, but not basal band extending caudad beyond postcubital stripe. Vein lines absent, with the exception of a basal, anal vein line expressed in some specimens, particularly prevalent in subspecies *gibsoni*. Hindwing - Ground colour extremely variable, ranging from white to pink, orange or yellow, although pinkish-orange in most populations; expression of dark markings variable ranging from extensive fusion of postmedial and subterminal elements to reduction of markings to only two or three postmedial spots. ***Male genitalia*** - Distal portion of valve varying from broad to slender, not constricted near middle, tapering to apex, apex rounded; saccular extension reduced; saccular process moderately developed; uncus broad-based, process evenly tapered to point, 2.3x longer than width of base; juxta slightly wider than long; aedeagus with dorsad curve at ⅔ distance beyond base; distal chamber of vesica kidney-shaped, coarsely scobinate; medial chamber ½ as wide as length of distal chamber, moderately scobinate; diverticuli moderately developed. ***Female genitalia*** - Ductus bursae unsclerotized; corpus bursae globose to slightly pear-shaped; four round, equal-sized signa; appendix bursae with angled elbow, not evenly coiled; posterior apophysis 1.5-2x longer than length of papillae anales.

Biology

Adults of *nevadensis* generally fly in late summer, with most records from late July to mid September. Subspecies *geneura* flies somewhat earlier, from early July to early August, with most records from late July. The earliest dates are for the northernmost populations (subspecies *vivida*), with records as early as late May and June, peaking in mid to late July. There is a single annual flight. Females do not come to light and as a result are very rare in collections.

Throughout its range, *G. nevadensis* prefers dry, often sparsely vegetated or eroding habitats. In the northern parts of its range subspecies *gibsoni* is very localized in occurence, found primarily in sandy prairie habitats such as partially stabilized dunes. *Grammia n. superba* is restricted to dry Garry Oak hills on Vancouver Island. *Grammia nevadensis geneura* occurs in mid- to high elevation dry, open forest habitat, while subpsecies *vivida* occurs on dry, sparsely vegetated south-facing slopes in montane grassland, particularly on sandy soil.

Distribution

Central British Columbia and Peace River region of Alberta south to eastern California and southern Nevada, east to southern Manitoba and Colorado (Fig. 2-114).

Molecular variation

Grammia nevadensis exhibits relatively large haplotype diversity with moderate divergences, although paraphyletic with respect to most species in the Western lineage, discussed in detail in Chapter 3. Eleven haplotypes occured among the 22 specimens sampled from 16 locations across the species' range, differing at most by 2.9% (Table 2-2). Despite the paraphyletic pattern of haplotype distributions, only one haplotype was shared with another species, *G. behrii*, (BH3; Fig. 2-133).

A short series of specimens from Hinsdale County, Colorado (9350' elevation) representing subspecies *geneura* had haplotypes (NV9, NV10) at least 1% divergent from all other Western lineage haplotypes (Fig. 2-133), including other *nevadensis* haplotypes.

The sampled population and topotypical *geneura* populations are separated by several mountain ranges and a distance of several hundred km, so it is possible that the sampled population is not *geneura,* but another unrecognized taxon in the *nevadensis* group; more specimens from mid- to high elevation are needed from CO.

Remarks

Grammia nevadensis exhibits a bewildering array of phenotypic variation, and mtDNA divergences unusually large for a given species. However, it seems most appropriate to treat this variation as a single species consisting of several subspecies, for the reasons outlined in Ferguson & Schmidt (2007) and the molecular variation discussed in Chapter 3. Briefly, the populations show clinal geographic variation into one another, and the molecular variation does not support a multi-species complex interpretation.

The superficial similarity of this species (particularly of subspecies *G. nevadensis geneura*) to *G. incorrupta* has resulted in long-standing taxonomic confusion. Although the morphological differences are slight, the overall differences in phenotype, ecology, behaviour and molecular variation leave little doubt that these represent different species.

GRAMMIA NEVADENSIS NEVADENSIS (GROTE AND ROBINSON)

FIGS. 2-22A, B.

Diagnosis

This is the smallest and palest of the *G. nevadensis* subspecies, the hindwing white to pale pinkish-white, the subterminal band absent or reduced to one or two marginal spots, medial and antemedial spots reduced or absent (well-developed in other ssp.). in most specimens, the forewing has a complete set of bands, and the thorax is entirely dark (the striped thorax form becoming more frequent in the northern and eastern Great Basin).

Distribution

The Great Basin region of the western United States, from OR and ID south through NV, east of the Sierra Nevada, CA east through UT to western CO. I have not specimens from AZ, but it occurs in Kane and Washington counties, UT and should occur in northwestern AZ.

Remarks

Some populations from north-central Oregon (Madras, Umatilla, John Day River) exhibit variation from *G. n. superba* to *G. n. nevadensis* phenotypes, and populations in northwestern Colorado (Moffat County) exhibit similar variation from *G. n. nevadensis* to *G. n. superba* and *G. n. gibsoni* phenotypes, including individuals intermediate between all-dark and striped thoracic vestiture, wherein the whitish stripes are darkened considerably. I interpret this variation as gradation into subspecies *superba* and *gibsoni*, respectively. The dark-thorax form is typical of subspecies *nevadensis*, and it apparently does not occur north of Washington state.

GRAMMIA NEVADENSIS SUPERBA (STRETCH)

FIGS. 2-22C, D.

Diagnosis

Grammia superba is on average larger, with narrower, more yellowish forewing bands; the hindwing is bright orange-red with more extensive dark markings compared to other *nevadensis* subspecies. The dark-thorax form is not known to occur.

Distribution

Vancouver Island, British Columbia, and likely also other islands in the Strait of Georgia.

Remarks

Although the name *superba* has been broadly applied to Pacific Northwest populations of *G. nevadensis* (Figs. 2-22 e,f), true *G. n. superba* exhibits a distinct phenotype restricted to Vancouver Island, BC, and possibly some of the adjacent gulf islands. It is disjunct from mainland *G. nevadensis*, the nearest populations occuring east of the coastal rain forests and Cascade Ranges in BC and WA.

GRAMMIA NEVADENSIS GENEURA (STRECKER)

FIG. 2-22I.

Diagnosis

Compared to other *G. nevadensis* subspecies, *G. n. geneura* is larger with a slightly broader wing shape, and flies earlier in the summer. The hindwing ground colour is distinctly pink.

Distribution

North-central to southwestern Colorado.

Remarks

As discussed by Ferguson and Opler (2006) and Ferguson and Schmidt (2007), the holotype of *geneura* is not the same species as the large, pale, smooth-lined species that flies in AZ, NM and southward (*geneura* of authors). It is unclear if *geneura* represents geographic or habitat-induced variation within *G. nevadensis* (high latitude and elevation *G. nevadensis* populations are more brightly coloured and fly earlier in the season), or another cryptic species within nominal *G. nevadensis*.

GRAMMIA NEVADENSIS GIBSONI (MCDUNNOUGH)

FIG. 2-22H.

Diagnosis

Grammia gibsoni is characterized by broad, whitish-buff forewing bands, relatively narrow wing shape, dark pink hindwings, and the absence of the dark thorax form.

Distribution

Distributed throughout the northern and central Great Plains, from southern AB, SK and MB south to at least central WY.

GRAMMIA NEVADENSIS VIVIDA SCHMIDT, NEW SUBSPECIES

FIG. 2-22G.

Type Material

Holotype - ♂. CANADA: Alberta, Kootenay Plains Ecological Reserve, 52.003° N, 116.467° W. 26 July 2006. B.C. Schmidt and J. Dombroskie. ***Paratypes*** - 121 males. **Alberta:** Same data as holotype (110 males, CNC, UASM, BCSC); Kootenay Plains Ecological Reserve, 26 July 2006, A. Roe and L. Lumley (1 male, UASM); Shunda Mtn, Nordegg, 26 July 1998, J. Troubridge (1 male, CNC); Nordegg , 17 July 1917, K. Bowman (1 male, UASM); Jasper Lake dunes, 29 June 1994, J. Troubridge (1 male, CNC); Peace River canyon, Dunvegan, 14 August 2003, B.C. Schmidt (2 males, BCSC); same locality and collector, 7 August 2002 (2 males, UASM); some locality and collector, 30 May 2005 (2 males, BCSC). **British Columbia:** Peace River canyon, Clayhurst Ecological Reserve, 29 July 1997, J. Shepard (1 male, RBCM).

Etymology

The name *vivida* refers to the vivid hindwing colour of the subspecies which is deep pink or orange-pink, distinctive among all North American populations of *G. nevadensis*.

Diagnosis

The combination of the bright, saturated pink hindwing ground colour, the fusion of the postmedial spots and subterminal band into one broad band, and the often pinkish tinge of the pale thorax and forewing markings are distinctive among populations of *G. nevadensis*.

Description

Head - Vestiture, colour, and antennal structure similar to and described under *G. nevadensis*. Eye diameter at widest point averaging 7.91×10^{-1} mm ($n = 7$). Antennal scales dark brown in most specimens, with at least some pale buff scales along dorsal shaft and pectinations in about 30% of specimens. ***Thorax*** - Colour and vestiture as described under *nevadensis*; the all-dark thorax form does not occur, and in about half of the specimens of *vivida*, there is a light to moderate tinge of pink in the pale borders of the thorax, often accompanied by pinkish forewing bands. Underside as described under *G. nevadensis*, the yellow scales of the underside varying to pale buff in about 25% of the specimens. ***Abdomen*** - Pattern and colour as for *G. nevadensis*, the dorsal ground colour varying from orange to pink. ***Forewing*** - Forewing length averaging 15.9 mm ($n = 12$). Overall pattern and colour similar to *G. nevadensis superba*, but with medial band often wider, and pale bands often with a pink tinge. Fringe entirely pale buff, occasionally with small areas of dark brown. Underside with identical pattern but with slightly washed out colours and less crisp pattern. ***Hindwing*** - Dorsally orange to dark pink with black markings; subterminal band and postmedial spots usually fused into one broad band. Fringe entirely pale buff to yellowish, occasionally with limited areas of dark brown concolorous with subterminal band. Underside colours less bright and with a cast of yellowish scales basally, but otherwise similar to upperside. *Genitalia*: Indistinguishable from those of other *G. nevadensis* subspecies. Female unknown.

Distribution

Typical *G. n. vivida* occurs east of the Continental Divide, in the Rocky Mountain front ranges of Alberta, and the Peace River canyon of Alberta and British Columbia.

Remarks

Grammia nevadensis vivida shows some phenotypic characters that could be attributed to both *G. n. superba* of the Pacific Northwest and *G. n. gibsoni* of the northern Great Plains: the pink hindwing and slightly broader forewing bands are characteristic of *gibsoni*, while the overall broader wing shape and tendency to suffusion of the hindwing markings is seen in the northern populations of *superba*. This, and the fact that mtDNA haplotypes typical of both *superba* and *gibsoni* occur in *vivida* populations, suggest that *vivida* is derived from *superba* and *gibsoni* ancestral stock. The Peace River population averages slight smaller, with less saturated hindwing colours. I have purposely limited the type material to populations east of the Continental Divide; although some specimens of *nevadensis* populations from central and eastern BC approach *vivida* in appearance, these populations are more typical of the highly variable forms (transitional to subspecies *nevadensis*) that occur throughout most of the Pacific Northwest north of the Great Basin (fig. 2-22e,f).

GRAMMIA YUKONA **SCHMIDT, NEW SPECIES**

FIGS. 2-23, 2-115.

Grammia geneura (Strecker); Lafontaine and Wood 1997: 738.

Type Material

Holotype - ♂. Canada, Yukon Territory, Kusawa Lake, north shore, 60.604° N 136.134° W, 800 m, 27 June 2004, rocky sage/juniper slope, B.C. Schmidt (CNC). ***Paratypes*** - 7 ♂♂, 1 ♀. **Yukon:** same data as holotype, (5 males, BCSC, CNC); Klondike Hwy., 10 km s. Moose Creek, 4 July 1981, C. Dondale, sage slope. (1 male, reared, CNC); Klondike Hwy. km 572, UVL at edge of marsh, 63°32'N 137 °08'W, 7 August 1980, #800145 ROM Fld. Pty. (1 male, CNC); Richardson Mtns., 67°58'N 136°29'W, 28-30 June 1987, M. Polak and M. Wood (1 female, reared, CNC).

Etymology

This species is currently only known from the Yukon Territory, hence the name.

Diagnosis

Very similar to *G. nevadensis superba*, but smaller with paler, washed-out colours, particularly the thorax underside, which is buff-coloured in *G. yukona*, compared to yellow in *G. nevadensis*. Eye size and antennal branch length averages smaller in *G. yukona* than in *G. nevadensis*, and the geographic ranges of the two do not overlap. *Grammia yukona* flies about one month earlier than the northernmost *G. nevadensis* populations. See also 'Remarks' below for discussion of the relationship to *G. nevadensis*.

Description

MALE. ***Head*** - Vestiture, colour and antennal structure similar to and as described under *G. nevadensis*. Antennal scales predominantly dark brown, with at least some pale buff scales along dorsal side in five of nine specimens; longest antennal branches averaging 4.76×10^{-1} mm, 3.2x intersegmental distance ($n = 6$). Eye diameter at widest point averaging 6.61×10^{-1} mm ($n = 7$). ***Thorax*** - Underside pale buff to yellow-buff, paler than the yellow seen in other *nevadensis* populations, the all-dark thorax form is not exhibited in the type material, and like northern populations of ssp. *superba*, probably does not occur. Colour and vestiture otherwise as described under *G. nevadensis*. ***Abdomen*** - Pattern and colour as for *G. nevadensis*, except that the dorsal ground colour tends to be paler, varying from yellow-buff to pale orange. ***Forewing*** - Average forewing length 15.3 mm ($n = 7$). Overall pattern and colour similar to *G. nevadensis superba*. ***Hindwing*** - Dorsally, ground colour yellowish-buff to pale orange, postmedial and subterminal dark markings tending to be fused more so than in *superba*. Underside colours more washed out, and lacking the flush of yellowish basal scales evident in *superba* and *vivida*. *Genitalia*: Indistinguishable from those of *G. nevadensis;* distal portion of valve tapering to apex, apex rounded; saccular extension reduced; saccular process moderately developed; uncus broad-based, process evenly tapered to point, 2.3x longer than width of base; juxta slightly wider than long; aedeagus with dorsad curve at ⅔ distance beyond base; distal chamber of vesica kidney-shaped, coarsely scobinate; medial chamber ½ as wide as length of distal chamber, moderately scobinate; diverticuli moderately developed.

FEMALE. Only known from one reared specimen, which has crumpled, incompletely expanded wings. The ventral thoracic and leg vestiture is rubbed, but based on the wing pattern and colour, it is very similar to female *G. n. superba*. Most of both antennae are missing; antenna moderately biserrate, as in *G. nevadensis*.

Biology

The habitat of *G. yukona*, where known, is dry, rocky or eroding south-facing slopes, characterized by grasses, *Artemisia* L., and *Juniperus horizontalis* Moench. Adults have been collected between late June and early August. Adults are attracted to light, but due to the brief dark period of northern summers, *yukona* may also be day-active.

Distribution

Known from three localities in the Yukon: the Richardson Mountains in the northeast, the Klondike Highway in central YT, and Kusawa Lake near the British Columbia border (Fig. 2-115).

Molecular Variation

Two sequenced specimens from the type locality show identical haplotypes, and are at least 3.5% divergent from all sampled *G. nevadensis* populations (YK1; Fig. 2-133). Although this level of divergence is indicative of species-level differences, the extensive mtDNA polyphyly within the genus (Fig. 2-136), and the fact that two specimens of Yukon *G. quenseli* showed identical or very similar haplotypes (YK1, QE3; Fig. 2-133) illustrate that mtDNA does not provide conclusive evidence of the specific distinctness of *yukona*. Nevertheless, no haplotypes were shared with the geographically nearest populations of *nevadensis* from west-central Alberta and central British Columbia, suggesting that there is no gene flow between these populations, and that *yukona* is truely disjunct.

Remarks

Grammia yukona is closely related to *G. nevadensis*. However, I believe that the large range segregation, morphological differences and genetic distinctness of *G. yukona* are best interpreted as species- rather than subspecies-level differences, particularly in light of the Beringian glacial history. The northernmost populations of *G. nevadensis* in central B.C. and west-central Alberta (Peace River canyon) approach *G. yukona* in appearance in that they are smaller with duller colours compared to nominate *G. nevadensis superba* and *G. nevadensis vivida*. The range restriction of *G. yukona* to the Beringian ice age refugium in dry grassland-steppe habitat so prevalent during the last glacial maximum, and the genetic divergence from *G. nevadensis*, indicate that *G. yukona* is likely a Beringian glacial relict, derived from *G. nevadensis* populations to the south.

GRAMMIA BEHRII **(STRETCH)**

FIGS. 2-24, 2-58, 2-88, 2-116.

Arctia behrii Stretch, 1872: 75, pl. 3, f. 11-12.
Arctia shastaensis French, 1889a: 35.
Arctia shastanensis Hampson, 1901 [misspelling]
Callarctia nevadensis Smith, 1938a: 129.
Apantesis nevadensis (Grote & Robinson) [in part]; Franclemont 1983: 117.
Grammia behrii (Stretch); Ferguson *et al.*, 2000: 48; Ferguson and Opler 2006: 11; Ferguson and Schmidt 2007: 46.

Type Material

Arctia behrii: the original description was based on two male and two female syntypes from Downieville, [Sierra Co.], California [USA]. The types are lost, and a neotype was designated by Ferguson and Schmidt (2007). The type locality is Jackson Cr[eek], 39 50'N 120 39'W, Plumas Co[unty], California, USA.

Arctia shastaensis: based on one male specimen that was missing the hindwings and abdomen. The French types may be destroyed (Lafontaine and Poole 1991). The illustration in French (1889b: 162) however leaves little doubt as to the identity of this name. Type locality: Upper Soda Springs, Siskiyou County, near Mt. Shasta [California, USA].

Diagnosis

Most specimens of *G. behrii* are easily recognized by the very wide, complete antemedial band on the forewing, all-dark thorax, bright pinkish-red hindwing with markings reduced or absent, and the yellowish forewing bands. Additionally, it is larger overall compared to *G. nevadensis*, with which *G. behrii* is most likely to be confused. Some forms of *G. ornata* can be similar to *G. behrii*, but *G. behrii* lacks the hindwing antemedial markings of *G. ornata*, has longer antennal pectinations, and flies in late summer not spring.

Description

Head and Thorax **-** Entirely dark brown, almost black; Male antennae with dark brown and scattered yellow scales along pectinations; longest pectinations averaging 7.01 x 10^{-1} mm, 4.06 times longer than intersegmental distance ($n = 6$). Female antennae slightly biserrate, less so than in *G. nevadensis*. Thorax dark brown ventrally, vestiture of coxae and femora usually at least partly yellow, legs dark brown to black, may be marked with yellow. ***Abdomen*** **-** Dorsally concolorous with hindwing ground color, with middorsal and lateral segmental black spots, sometimes merging into a solid stripe; underside of abdomen black, segments bordered distally with transverse yellowish bands. Anal tuft black or mixed black and yellowish. ***Forewing*** **-** black, with the usual pattern of light bands typical of the *nevadensis* complex, except that their color is bright ochreous yellow, and the antemedial band is usually conspicuously wider than other bands, up to 5 mm wide; The medial band may be missing or reduced to one or more small spots at or near the position of the discal spot in other moths. The antemedial, medial (if present) and postmedial bands commonly cross the postcubital stripe to the anal margin, but the basal band never does. Fringes blackish, yellow tipped. Hindwing - Ground colour saturated orange-pink, rarely yellow. Dark markings usually reduced to two to three postmedial spots, and subterminal band reduced to narrow marginal black marks; Fringe yellowish. Sexes similar in wing pattern, females exhibiting brighter, more saturated colours as in other species of the *nevadensis* group. ***Male genitalia*** **-** Distal portion of valve gradually tapering to rounded apex; saccular extension poorly developed; saccular process moderately developed; uncus broad-based, process evenly tapered to point, 2.5x as long as width of base; juxta 1.75x wider than height, dorsal concavity broad, relatively deep; aedeagus with dorsad curve at ⅔ distance beyond base; medial chamber of vesica short, about as long as wide, minutely scobinate; distal chamber kidney-shaped, twice as long as wide, coarsely scobinate; diverticuli moderately developed. ***Female genitalia*** - Ductus bursae unsclerotized; corpus bursae slightly pear-shaped, 3x width of ostium bursa; signa round or ellipsoid, averaging about 2.5×10^{-1} mm, coarsely scobinate; posterior apophysis slightly longer than papillae anales.

Biology

Adults have been captured between early August and Late September, with most records from mid September. Females do not come to light, and are partially or entirely diurnal. Two female specimens from Los Angeles County were collected in flight in mid-afternoon. Larvae have been collected on *Lotus humistratus* E. Greene (Fabaceae) and *Amsinckia* (Boraginaceae) in Los Angeles County. *Grammia behrii* inhabits dry, low- to mid-elevation lithosol flood plains and balds in the Siskiyou – northern Sierra Nevada ranges, but is absent from serpentine barrens (J. Troubridge, pers. comm.).

Distribution

Occurs from Portland, Oregon south to Los Angeles and Kern Counties, California, with most records from the Siskiyou and Sierra Nevada ranges (Fig. 2-116). Ferguson *et al.* (2000) also gave a record for west-central Idaho.

Molecular Variation

Three specimens exhibited three haplotypes, all of which were paraphyletic with respect to *G. nevadensis* (Table 2-2, Fig. 2-133). *Grammia behrii* haplotypes showed a maximum of 0.9% intraspecific divergence, including one shared haplotype with *G. nevadensis* from central Washington (BE1; Fig. 2-133).

Remarks

Grammia behrii is a rarely collected species that was for many years relegated to the synonomy of *G. nevadensis*, but as discussed by Ferguson and Schmidt (2007), is a distinct species. The two are sympatric in Siskiyou County (Hornbrook) in northern California, and possibly also in the Greenhorn Mountains, Kern County.

GRAMMIA BRILLIANS SCHMIDT, NEW SPECIES

FIGS. 2-27, 2-60, 2-118.

Type Material

Holotype - ♂. Utah, [Garfield Co.], Bryce Canyon, Water Canyon, 6800', 10 July 2005, S. Mueller, DNA voucher # BCS-1087, 'barcode' voucher BCSC-244. [USNM].
Paratypes - 2 ♂♂. Same data as holotype [USNM, CNC]

Etymology

The name *brillians* reflects the bright, saturated colours of the hindwing.

Diagnosis

The wing pattern, colour and male antennal structure are most similar to *G. bowmani*, but *brillians* lacks antemedial and medial markings on the hindwings (usually present in *bowmani*), and the postmedial forewing band curves basad near the costa, not straight or nearly so as in *bowmani*. Internally, the medial and distal chamber of the male vesica are longer and more elongate in *brillians*, covered in smaller, more numerous spinules; the saccular process is reduced in *brillians*, well-developed in *bowmani*. In comparison, *Grammia williamsii tooele*, like *bowmani*, also has a straight postmedial forewing band, shorter male antennal pectinations, and fewer forewing bands. *Grammia nevadensis* is symaptric with *G. brillians*, but flies later in the season and has longer male antennal pectinations, and symaptric *G. nevadensis* populations have much paler and washed-out colours, and are unlikely to be confused with *G. brillians*.

Description

Head - Frons, vertex and palps entirely dark brownish black; eyes fully developed; male antennae moderately bipectinate, pectinations averaging 5.42×10^{-1} mm, 3.4 times longer than intersegmental distance ($n = 2$); antenna with dark brown dorsal scales, or dark brown with buff scales near apex of pectinations. ***Thorax*** - Vestiture entirely dark brownish black dorsally and ventrally; a few light brown scales at base of forecoxa; legs entirely dark brown with buff apex of tibia. ***Abdomen*** - Ground colour pink dorsally with buff scales at apical tuft, medial and lateral markings brownish black; predominantly black ventrally, segments with buff lateral and distal margins. ***Forewing*** - Mean forewing length 16.1 mm (*n* = 2 males); ground colour dark brownish black, fringe variable, entirely pale buff or black and buff; bands ivory in colour, antemedial band incomplete, extending toward inner margin beyond postcubital stripe; medial and postmedial bands curved basad near costa, extending beyond postcubital stripe when well developed; similar ventrally, with colours less bright and a slight yellowish flush near wing base. Hindwing - Ground colour bright orange-pink, patterned with black; antemedial and medial markings absent, or medial markings reduced to a single, indistinct discal spot; postmedial spots variable, but relatively reduced, not confluent with subterminal markings; fringes variably black and buff; at anal angle; ventral and dorsal pattern similar, colours less bright ventrally and with a slight yellow flush near wing base. ***Male genitalia*** - Distal portion of valve tapering evenly to more or less rounded apex; saccular process poorly developed, saccular process reduced; uncus long evenly tapered, typical of genus; juxta broad nearly twice as wide as high; aedeagus relatively broad, distal end curving dorsally, and opening to the right as in other *Grammia*; vesica with kidney-shaped distal chamber, relatively elongate medial chamber; medial and distal chamber scobinate, spinules relatively small.

Female: unknown.

Biology

Adults come to light, and the type series was collected on July 10, the only known flight date. Nothing else is known of its biology.

Distribution

Known only from the type locality in Bryce Canyon National Park, Utah (Fig. 2-118).

Molecular Variation

The single sequenced specimen exhibited a unique haplotype, at least 0.8% divergent from other haplotypes in the western lineage (Table 2-2; Fig. 2-133).

Remarks

Although I hesitate to describe a species from only three specimens taken at a single locality, particularly in such a phenotypically variable group, it is clear from the morphological and molecular data that this taxon is distinct from other species in the *nevadensis* group. *Grammia brillians* may be endemic to southern Utah; a similar pattern of endemism is seen in the noctuids *Protogygia pectinata* Lafontaine and *Copablepharon opleri* Lafontaine (Lafontaine 2004). The complex geological history of the Colorado Plateau and the edges of the Great Basin likely played an important role in the evolutionary radiation of the *nevadensis* group.

GRAMMIA FERGUSONI SCHMIDT, NEW SPECIES

FIGS. 2-35, 2-68, 2-92, 2-126.

Type Material

Holotype **-** ♂: California, Inyo County, Mono Pass, 12,000', 1 August 1978, C.D. MacNeill [CNC]. ***Paratypes*** **-**7♂♂ 6♀♀. **California**: Tuolumne County, Sonora Pass, 9623', 20 July 1953, T.W. Davies [LACM]; Tuolumne County, Leavitt Peak, 11050-12000', 29 August 1967, P. A. Opler, 1♂ [UCB]; Tuolumne County, near Sonora Pass, Leavitt Peak, north slope, 10,500', 22 August 1975, J. Wiseman, 1♂, [LACM]; Mono County, Lake Marie, 12 August 1944, R. Mattoni, 2♀♀ [LACM]; Mono County, White Mtns., Blanco's Corral, 10,000', 7 July 1953, D.D. Linsdale, 1♂ [UCB]; Inyo County, Mono Pass, 12,000', 1 August 1978, C.D. MacNeill, 1♀ [CNC]; same locality, 10 August 1958, J.M. Burns, 1♂ [UCB] same locality and date, C.D. MacNeill, 1♀ [UCB]; Mono County, White Mtns, Barcroft, 13,000', 28 July 1958, C.D. MacNeill & W.W. MacGuire, 1♂1♀ [USNM]; Fresno County, Mono Pass, 37.424°N 118.771°W, 12040', larva coll. 18 August 1998, reared on *Taraxacum*, L. Crabo, 1♀ [Lars Crabo personal collection].

Etymology

The name honours the late Douglas C. Ferguson, whose research has contributed significantly to the state of knowledge of North America's arctiid moths.

Diagnosis

Grammia fergusoni is relatively distinctive among *Grammia*, and somewhat resembles a small, "pointy-winged", brightly coloured *G. nevadensis* or *G. behrii*. The antennae are buff-coloured, not brown-black as in most *nevadensis* group species, and the male antennal pectinations are shorter than in *G. nevadensis*. The forewing is more pointed and elongate apically, and the hindwing more triangular. Internally, the male distal portion of valve is slightly hooked, not blunt or rounded. This species is diurnal, and is endemic to the alpine zone of the central Sierra Nevada.

Description

Head - Vestiture of frons pale buff with black lateral border, vertex and palps black with pale buff borders; eyes reduced, averaging 5.8 x 10^{-1}mm at greatest diameter; male antennae moderately bipectinate, pectinations averaging 3.3 x 10^{-1} mm, 2x times longer than intersegmental distance (n = 3); antenna with pale buff dorsal scales, apical third of antenna black; female antennae slighty bipectinate. ***Thorax*** - Vestiture black with narrow, pale buff borders on vertex, patagia and tegulae; dark brown to black ventrally with yellowish buff central tuft at base of forecoxae; legs predominantly pale buff, femur dark brown basally with yellowish buff apical half. ***Abdomen*** - Ground colour pinkish-orange, pale buff near apex; medial and lateral markings dark brown to black; pale buff ventrally, dark brown to black markings consisting of two rows of spots; females with ventral spots expanded and confluent, segments pale bordered distally. ***Forewing*** - Male forewing shape elongated toward apex, mean forewing length 14.4 mm (n = 3), females considerably larger with somewhat broader wing shape, forewing length 17.7 mm (n = 2); ground colour dark chocolate brown, fringe pale buff; banding pattern complete or with antemedial band reduced to costal spot and line caudad of postcubital stripe; medial band often wider than postmedial, the latter curved basad near costa as in *G. nevadensis* group. Hindwing - Ground colour bright pinkish-orange, patterned with black; antemedial and medial markings often extending basally as a dash in males, reduced or absent in females; postmedial and subterminal markings usually confluent in males, discrete in females; fringe pale buff to orange, particularly near anal angle; ventral pattern similar to dorsum, colours slightly paler. ***Male genitalia*** - Distal portion of valve narrowing gradually, apex slightly hooked, point of hook directed ventrad; saccular process and ventral process well-developed; uncus broad-based, process evenly tapered to point; juxta 1.5 – 2x wider than long; aedeagus with dorsad curve at ⅔ distance beyond base; vesica overall most similar to *G. nevadensis*, curving dorso-cephalad; distal chamber of vesica relatively elongate and kidney-shaped, scobinate, spinules relatively large. ***Female genitalia*** - Not examined.

Biology

Adult dates of capture are primarily in August, with a few in mid July. This is a diurnal species that flies in subalpine and alpine habitat.

Distribution

Known only from the central Sierra Nevada and White Mountains in California (Fig. 2-126).

Molecular Variation

Not examined.

Remarks

The small size, narrow wing shape and antennal structure and colour suggest a close affinity to *G. blakei*, although the vesica structure is unlike this species, and is more typical of *G. nevadensis*.

GRAMMIA BOLANDERI (STRETCH)

FIGS. 2-31, 2-130.

Arctia bolanderi Stretch, 1872: 76, pl. 3, fig. 13.

Apantesis bolanderi (Stretch); Franclemont, 1983: 117.

Grammia bolanderi (Stretch); Ferguson and Opler 2006: 10.

Type Material

Described from a single male from Mt. Shasta [Siskiyou Co.], California [USA], and like most of Stretch's type material, is presumed lost.

Diagnosis

Resembles *G. williamsii*, but the more elongate forewing shape, lack of hindwing antemedial and medial spots, and discrete rather than confluent postmedial and subterminal markings, in addition to its small size, distinguish *G. bolanderi*; *G. williamsii* is not known to occur west of the Cascade/Sierra Nevada crest. The small size and overall pattern approach *G. fergusoni*, but the straight versus curved postmedial line, lack of hindwing antemedial and medial spots (well developed in *G. fergusoni*), hindwing ground colour (pink vs. reddish orange) suggest these species are not conspecific. See 'Remarks' below.

Description

Head, Thorax, Abdomen – unknown; although the head, antennae and markings of the thorax and abdomen are clearly visible in the illustration accompanying the original description, Stretch (1872) notes in the text description that "the condition of the body parts of the only specimen I have seen, is such as to preclude an accurate description." This calls into question the accuracy of the illustrated specimen. The thorax and abdomen are depicted with the light and dark striped pattern typical of the genus, but no written description is given. The antennae appear thickened, presumably slightly bipectinate. ***Forewing*** - Wing expanse given as 1.00 inch, which corresponds to a forewing length of about 12 mm; ground colour blackish brown, fringes, costa, and anal margin yellowish; antemedial band restricted to wedge at costal margin; medial, postmedial, subterminal bands and postcubital stripe well developed; medial and postmedial confluent at and extending through postcubital stripe; bands dirty yellowish in colour; anal dash absent. Hindwing - Ground colour described as rose, markings black, consisting of three postmedial spots and partial subterminal band; fringes yellowish; ventrally with similar pattern but more yellowish colour overall, hindwing ground colour orange-rose. *Genitalia:* unknown.

Biology

Unknown. *Grammia bolanderi* is most similar to *G. williamsii* and *G. blakei*, and, like these species may fly in spring or early summer. May be diurnal.

Distribution

Known only from Mt. Shasta, California, the type locality.

Molecular Variation

No data available, no extant specimens.

Remarks

Little additional information on *bolanderi* has come to light since Marion Smith remarked that "its specific standing must remain in question" nearly 70 years ago (Smith 1938a). Although the type specimen is lost, the original description and accompanying illustration leave little doubt that *bolanderi* is distinct from any other species known to occur in northern California and the Pacific Northwest. Earlier authors often associated it with *G. blakei*, but the differences in markings, colouration, habitat and geographic range preclude synonomy with this species. The small size, forewing shape, straight postmedial band, and absence of basal and antemedial bands are characteristic of *G. williamsii*, but the loss of hindwing antemedial and medial elements is rare in *G. williamsii*, particularly males. Also, *G. williamsii* is not known to occur west of the Cascade / Sierra Nevada ranges, with the nearest records to the southeast of Mt. Shasta, in Sierra County on the east slope of the Sierra Nevada. Given the phenotypic and biogeographic differences, *G. bolanderi* does not appear to be a synonym of *G. williamsii*. Until specimens from the vicinity of the type locality can be examined, the taxonomic status of this enigmatic *Grammia* will remain uncertain.

GRAMMIA WILLIAMSII (DODGE)

FIGS. 2-28, 2-62, 2-89, 2-120.

Arctia williamsii Dodge, 1871; Canadian Entomologist, 3: 167

Arctia determinata Neumögen, 1881b; Papilio 1: 28

Apantesis tooele Barnes and McDunnough, 1910; Canadian Entomologist, 42: 208-209;

Apantesis tooele ab. *ophir* Barnes and McDunnough, 1910; Canadian Entomologist, 42: 208-209

Apantesis bolanderi ab. *confluentis* Strand, 1919; Lepidopterorum Catalogus, 22: 283

Revised Synonymy.

Apantesis bolanderi confluentis Strand; Franclemont 1983: 117.

Apantesis williamsii (Dodge); Franclemont, 1983: 117.

Apantesis williamsii tooele (Barnes and McDunnough); Franclemont, 1983: 117.

Grammia williamsii (Dodge); Ferguson and Opler 2006: 10.

Grammia williamsii tooele (Barnes and McDunnough); Ferguson and Opler 2006: 10.

Type Material

Arctia williamsii: described based on a single female specimen from "Colorado Territory". The specimen is presumed lost or destroyed. An illustration is given in the original description, although according to Dodge (1871) himself, the illustration did not exactly match the specimen. However, the text description and illustration are consistent with the current concept of *williamsii*. In order to preserve the current usage of the name *williamsii* for this taxon, a male specimen bearing the following labels is hereby designated as **neotype:** "le.g. D.E. B[owman]. J[u]ne./ 15, 1990 Blacktail/ Creek Grand Co./ Colorado", "NEOTYPE/ *Arctia/ williamsii* Dodge/ B.C. Schmidt 2007" [CNC].

Arctia determinata was described based on an unstated number of specimens, collected by H.K. Morrison in 1877, and in 1880 by J. Doll and B. Neumögen, in "middle and southern Colorado" (Neumögen 1881). Two male syntypes are in the USNM, one labeled "Feb.8.81/ Arctia/ determinata/ Neumögen/ Type.", "Col./ B. Neumögen.", " Col.", "TYPICUM/ SPECIMEN" [examined], another with identical labels, in addition to the following: "Arctiidae / genitalia slide/ No. AW1010", "Type No. 33678/ U.S.N.M." [examined].

Apantesis tooele: described from six male syntypes from Provo and Eureka, Utah. The male specimen in the USNM [examined] labelled Provo Utah/ VII-4-9/ Tom Spalding", "Apantesis/ tooele/ B and McD/ Type ♂", "Arctiidae/ genitalia slide/ No.AW1011", "LECTOTYPE/ *Apantesis tooele*/ Barnes and McD./ B.C.Schmidt 2007" is hereby designated as **lectotype** to ensure consistency in the application of the name to this taxon, and to avoid confusion with similar species.

Apantesis tooele ab. *ophir*: based on five male specimens of the form with entirely black thoracic vestiture; the name *tooele* has page priority. *ophir* was described as an abberational form, and is therefore an unavailable infrasubspecific name.

Apantesis bolanderi ab. *confluentis*: Strand (1919) based this name on Hampson's (1901: 405) concept of *bolanderi*. It is clear from Hampson's description that he was referring to *Grammia williamsii*, and the "abberation" he describes fits the description of *G. williamsii* with well-marked hindwings. In turn, Hamspon's concept of *G. williamsii* (as *Apantesis viallimsi* [sic]) fits the description of *G. nevadensis*, and not *G. williamsii*. Strand (1919) named *confluentis* based on Hamspon's *Apantesis bolanderi* Ab. 1 (Hampson, 1901: 405-6).

Diagnosis

Grammia williamsii is one of the most common and widespread members of the genus, and can be difficult to recognize in parts of its range due to the variation in hindwing colour and hindwing dark markings. The reduced forewing banding pattern, straight (or nearly straight) postmedial line, broad, 'stubby-looking' wings are diagnostic; curiously, *G. williamsii* males often also have a smaller abdomen relative to overall size compared to other *Grammia*. In the western United States, *G. williamsii* could be confused with *G. bowmani*, *G. yavapai*, or *G. favorita*, and additional diagnostic differences are given under these species. Other similar species include *G. franconia* and *G. margo*, from which it can be quickly be distinguished by the longer male antennal pectinations and later flight season of *G. williamsii*; see 'Diagnosis' under *G. margo* and *G. franconia* for additional characters. In eastern Canada/northeastern U.S., some forms of *G. figurata* can look like *G. williamsii*, but *G. figurata* has a more rounded wing shape, and the distance between the medial and postmedial lines at the costa is greater in *G. figurata*. The ranges and habitats of *G. williamsii* and *G. figurata* are not known to overlap, with *G. williamsii* occuring in northern boreal forest habitats. See also *G. bolanderi*.

Description

Head - Vestiture of frons and vertex black, pale buff laterally; eyes well developed, diameter averaging slightly smaller in females than in males; (eyes strongly reduced in two females from Colorado and California at high elevations); male antennae moderately bipectinate, pectinations averaging 4.66 x 10^{-1} mm, 2.96 times longer than intersegmental distance ($n = 6$); antenna with dark brown dorsal scales, occasionally with scattered buff scales; female antennae biserrate to slighty bipectinate. ***Thorax*** - Vestiture dark brown to black with broad, pale buff to pinkish buff borders on vertex, patagia and tegulae; entirely dark thorax forms occur in subspecies *tooele*; dark brown to black ventrally with yellowish to pinkish buff central tuft at base of forecoxae; legs predominantly dark brown with pale buff, varying to mostly pale buff. ***Abdomen*** - Dorsal ground colour pale pink to yellowish buff in males, yellow to pinkish orange in females, pale buff near apex; medial and lateral markings dark brown to black; pale buff ventrally, dark brown to black markings consisting of two rows of broad spots, sometimes broad and converging medially; females entirely dark brown ventrally. ***Forewing*** - Mean forewing length 14.9 mm ($n = 6$); ground colour chocolate brown to dark brown, discal cell area often darker; banding pattern reduced, basal band absent, antemedial usually absent or reduced to costal spot; medial band usually present, extending to but not beyond postcubital stripe; postmedial nearly always present, straight near costa and with little or no change in angle at M_3 vein; band colour pale to pinkish buff; fringe variable in colour, dark brown to pale buff; costa entirely dark brown or with variable amount of thin, pale buff border; anal margin usually white at least halfway to anal angle; anal dash absent in >95% of specimens; underside similar to upperside, but bands less contrasting; sexes similar. Hindwing - Ground colour varying from dull orange-buff to pinkish buff, rarely yellowish, most commonly dull pink; brighter yellowish to pinkish orange in females; markings dark brown to black, well developed and often confluent, particularly postmedial and subterminal markings; antemedial markings well developed, often streaked towards wing base; ventrally with similar pattern and duller ground colour; females with reduced hindwing spots and brighter, often orange-pink, ground colour. ***Male genitalia*** - Distal portion of valve gradually tapering to rounded apex; saccular extension moderately developed, saccular process moderately developed; uncus broad-based, process evenly tapered to point; juxta wider than long; aedeagus with dorsad curve at ⅗ distance beyond base; distal chamber of vesica nearly globose, slightly kidney-shaped, scobinate, spinules relatively large; medial chamber roughly as wide as distal chamber. ***Female genitalia*** - Ductus bursae unsclerotized; corpus bursae more or less globose and relatively small, 2-2.5x width of ostium bursa; signa equal, round and relatively small (2.56×10^{-1} mm); appendix bursae with broad, angled elbow, not evenly tapered; posterior apophysis 1.5x longer than length of papillae anales.

Biology

Collection dates of adults range from mid May to late August, depending on altitude and habitat. Most records from the Great Plains are from June, while boreal and mountain populations peak in July. Although this species is often the most common *Grammia*, I have seen few females, all reared, and they are not attracted to light, or are unable to fly to light when gravid. Larvae likely feed on many dicots and occasionally grasses; wild caught larvae have been recorded on *Thermopsis rhombifolia* (Fabaceae), *Senecio* (Asteraceae), *Delphinium bicolor* (Ranunculaceae) and *Triticum aestivum* (Poaceae) (Byers 1988, BCS, pers. obs.). Widely distributed, and found in montane and prairie grasslands, dry subalpine meadows, and dry (often sandy) boreal forest.

Distribution

Occurs from the Northwest Territories east to the northern Great Lakes region, New Brunswick, and New England. Occurs throughout the northern Great Plains, and south at higher elevations to Arizona and New Mexico, west to southeastern British Columbia and eastern California (Fig. 2-120).

Molecular Variation

As discussed in Chapter 3, *G. williamsii* exhibits a phenomenal range of geographically structured variation in *cox1* haplotypes, representative of two divergent mtDNA lineages within the genus (Fig. 2-99). Forty-nine specimens representing populations from all geographic regions within the species' range showed 23 haplotypes, with a mean divergence of 2.5%, up to divergences of 6.5% (Table 2-2, 2-3). The six specimens of *G. williamsii tooele* from two localities exhibited two unique haplotypes (WI12, WI13), surprisingly divergent from *G. williamsii*, and indeed all other *Grammia* (Fig. 2-133), with the most similar haplotype about 3% divergent (Fig. 2-133). Northeastern Nevada individuals of *G. williamsii*, geographically adjacent to the *G. w. tooele* sample sites, had a haplotype (WI14) more similar to other *G. williamsii* haplotypes in the Western lineage (Fig. 2-133).

Remarks

This species is often the most abundant *Grammia* in the western parts of its range. Although it is also one of the most widespread species, it expresses relatively little geographically structured phenotypic variation, and often considerable variation within a population. In long series, boreal and mountain populations tend to have a pinker hindwing with suffused and expanded dark markings, compared to the Great Plains populations which show a reduction in the hindwing markings with a duller, often orangish ground colour and slightly larger wing span.

GRAMMIA WILLIAMSII WILLIAMSII (DODGE)

FIGS. 2-28A - D.

Diagnosis

Nominate *G. williamsii* shows relatively little geographic variation, but see 'Remarks' under *G. williamsii* above. See Diagnosis under *G. williamsii tooele* for comparison to this subspecies.

Distribution

The range of this subspecies is here considered to include the majority of the species' range as given under *G. williamsii*, with the exception of central Utah, where *tooele* occurs.

GRAMMIA WILLIAMSII TOOELE (BARNES AND MCDUNNOUGH)

FIG. 2-28E.

Diagnosis

This subspecies is distinguished from nominal *williamsii* by the occurence of the dark thorax form, reduced hindwing dark markings, slightly larger size and brighter orange-pink hindwing ground colour.

Distribution

Central Utah, from Cache county south to Beaver county.

Remarks

Grammia williamsii tooele was originally described as a species distinct from *williamsii*, distinguished by the black thorax, brighter hindwing colour, and larger size compared to *williamsii*. Barnes and McDunnough (1918) subsequently relegated *tooele* to subspecies status of *williamsii*, and the status of *tooele* has subsequently remained unchanged.The absence of shared haplotypes with, and significant *cox1* sequence divergence from *G. williamsii* suggest *G. w. tooele* could be distinct species, but I am unable to find consistent morphological differences separating the two taxa in Utah, with significant overlap in size and hindwing colouration. Specimens from some populations exhibit variation from *tooele* to *williamsii* phenotypes, although the absence of *tooele* phenotypes in eastern Nevada is noteworthy. It is possible that the dark-thorax form is a result of past or ongoing hybridization with *G. nevadensis nevadensis*, supported by the fact that Nevada samples of *G. w. williamsii* displayed haplotypes virtually identical to two *G. n. nevadensis* haplotypes from Utah and southeastern Oregon (Fig. 2-133).

Conversely, this does not explain the molecular divergence between Utah *G. w. tooele* and *G. w. williamsii* from adjacent parts of Nevada (Fig. 2-133). Based on the apparent intergradation of *toolele* and *williamsii* phenotypes, geogrpahically restricted occurence of the dark thorax (nominate *tooele*), and the distinct *cox1* lineage, I treat *tooele* as a subspecies. Extensive sampling of key geographic areas would shed some light on this interesting situation, namely where *tooele* and *williamsii* should overlap or intergrade in western and central / northcentral Utah.

GRAMMIA FAVORITA (NEUMÖGEN)

FIGS. 2-29, 2-65, 2-123.

Arctia favorita Neumögen, 1890b: 173.
Apantesis favorita (Neumögen); Franclemont 1983: 117.
Grammia favorita (Neumögen); Ferguson and Opler 2006: 11.

Type Material

Arctia favorita: described from two male syntypes from Idaho Springs, Colorado [USA]; in order to stabilize the name, the male syntype with the following labels is hereby designated as **lectotype** [USNM, examined]: "Colo./ Bruce.", Col./ B. Neumögen.", "Arctia/ favorita-/ Type. Neumgn.", "TYPICUM/ SPECIMEN", Lectotype No./ 33676/ U.S.N.M.", "Arctiidae/ genitalia slide/ No. AW1008", "LECTOTYPE/ Arctia/ favorita Neumgn./ B.C. Schmidt 2007". Although the specimen bears a previous lectotype catalogue number, there are no previous published lectotype designations.

Diagnosis

Grammia favorita can resemble a brightly marked, unlined form of *G. phyllira*, but the presence of an antemedial band, the extension of all or most of the transverse bands past the anal margin of the postcubital stripe and the narrower wing shape will distinguish *G. favorita*. The hindwing is brighter pink in *G. favorita* than *G. phyllira*, and it lacks the distinct pink cast of the ventral wing surface of *G. phyllira*. Variants of *G.*

williamsii with reduced markings on a saturated pink hindwing come close in appearance, but the wide forewing bands, including an antemedial, are diagnostic of *G. favorita*. This species is known only from the central Great Plains where it occurs in sandy prairie habitat together with *G. williamsii*.

Description

Head - Palps black; frons and vertex pinkish buff, vertex black centrally; male antennae strongly bipectinate, pectinations averaging 5.81 x 10^{-1} mm, ($n = 2$); dorsal scales dark brown to black; eyes well developed, mean diameter 1.02 mm ($n = 2$). ***Thorax*** - Vestiture black with pinkish to creamy buff borders on vertex, patagia and tegulae; sides of thorax dark brown ventrally, with extensive pink vestiture at base of coxae; legs buff-coloured with extensive black markings. ***Abdomen*** - Dorsal ground colour deep pinkish red, apex not noticeably paler; medial and lateral markings black; pale buff ventrally, lateral black spots relatively large but not confluent. ***Forewing*** - Relatively narrow, in shape more similar to *nevadensis* group than *G. phyllira*; male forewing length averaging 17.7 mm ($n = 2$ males); dark brown to black dorsally, vein lines absent, except occasionally at base of anal vein; bands rich creamy buff to pinkish buff; antemedial, medial, postmedial, subterminal bands and postcubital stripe generally well developed, often broad and with irregular margins; antemedial sometimes fragmentary; transverse bands extending at least slightly beyond postcubital stripe; fringe entirely cream, costa variably cream and dark; anal margin with relatively broad cream line; ventral markings similar, but dark colours slightly paler and with a slight yellowish cast basally. Hindwing - Ground colour deep pinkish red; black markings reduced to moderately developed, postmedial spots discrete; subterminal band irregular, broadest at distal apex and generally absent in anal angle; antemedial spots absent or reduced, medial discal spot variable, from well-defined to absent; fringe pink and pale buff; ventral dark markings slightly paler but otherwise similar to dorsum. Female not examined. ***Male genitalia*** - Distal portion of valve with tapered to broadly rounded apex; saccular extension poorly developed, saccular process moderately developed; uncus broad-based, process evenly tapered to point, 1.5-2x as long as width of base; juxta 1.5 x wider than long, dorsal margin with shallow, broad u-shaped concavity; aedeagus with dorsad curve at ⅔ distance beyond base; vesica with basal and medial chamber approximately equal in length and width, not scobinate; distal chamber relatively small, slightly longer than width of medial chamber, kidney-shaped, coarsely scobinate; vesica slightly longer than aedeagus. ***Female genitalia*** **-** Not examined.

Biology

Adult collection dates for *G. favorita* range from mid May to mid June. *G. favorita* occurs in prairie sand dunes of the central Great Plains. I have not seen female *G. favorita* specimens, and like most *nevadensis* group species, these may not come to light or may be unable to fly when gravid.

Distribution

Grammia favorita appears to have a very limited distribution, occuring only in sand hill prairie. I have seen specimens only from the Nebraska Sand Hills, Nebraska and northeastern Colorado (Fig. 2-123).

Molecular Variation

Only one specimen of *favorita* was available for analysis, and exhibited an Eastern lineage haplotype (EA33), differing by only one or two base pairs from several *G. virguncula* and and one *G. williamsii* haplotype (Fig. 2-134).

Remarks

Although previously associated with *G. phyllira*, the forewing pattern, lack of the ventral forewing pink cast, coarsely scobinate male vesica and mtDNA haplotype suggest *favorita* is more closely related to *G. williamsii* and the *nevadensis* group than *G. phyllira*.

GRAMMIA ELONGATA (STRETCH)

FIGS. 2-34, 2-63, 2-90, 2-121.

Arctia elongata Stretch, 1885; Entom. Amer. 1: 105

Arctia dieckii Neumögen, 1890a; Entom. Amer. 6: 62

Apantesis elongata (Stretch); Franclemont 1983: 117.

Grammia elongata (Stretch); Ferguson and Opler 2006: 10.

Type Material

Arctia elongata: described from a female holotype [lost?]. Smith (1938a) states the holotype is in the USNM (type # 33680), but I was unable to locate it in 2005. The type locality is Spokane Falls, Washington, USA.

Arctia dieckii: based on one male specimen, USNM type no. 33677 [examined]. The type locality is Spence's Bridge, Brit[ish] Col[umbi]a, [Canada].

Diagnosis

Similar to *Grammia williamsii*. However, nearly all specimens of *elongata* can be distinguished by the presence of a pale-lined forewing cubital vein (not lined in *williamsii*), hindwing anal dash (rare in *williamsii*), curved postmedial forewing band, and more elongate wing shape compared to *G. williamsii*. The hindwing ground colour is pale yellowish, never with orange or pink colours as in most *G. williamsii*. Eye size is also reduced in *elongata* (< 0.60 mm diameter, > 0.60 mm in *G. williamsii*). *Grammia elongata* is restricted to subalpine meadows, flying above 6000' elevation, while *G. williamsii* occurs in lower elevation dry grassland habitats, although the two species can occur together in the southern Alberta foothills.

Description

Head - Vestiture of palpi, frons, and vertex varible in colour, ranging from entirely black to entirely pale buff; palps, frons and vertex black, pale bordered; eyes reduced, lateral margins of eyes with exposed gena, mean maximum eye diameter 5.68×10^{-1} mm (n = 6 males); male antennae moderately bipectinate, pectinations averaging

4.17×10^{-1} mm, 2.6 times longer than intersegmental distance ($n = 6$); dorsal antennal scales variable in colour, dark brown or pale buff; female antennae biserrate to slighty bipectinate. ***Thorax*** - Vestiture dark brown to black with broad, pale buff borders on vertex, patagia and tegulae; pale buff ventrally, central tuft yellowish buff, dark brown to black laterally; legs predominantly pale buff with segments black basally. ***Abdomen*** - Dorsal ground colour pale yellowish buff, pale buff near apex; medial and lateral markings black, medial line relatively wide; occasionally entirely black in females; pale buff ventrally, black markings consisting of two rows of broad spots, these confluent in females resulting in entirely black or black, buff bordered abdominal segments. ***Forewing*** - Mean forewing length 14.9 mm ($n = 6$); ground colour brownish black, discal cell area often with slightly darker streak; banding pattern reduced, basal band absent, antemedial absent, reduced to costal spot; medial band usually present, extending to and occasionally slightly beyond postcubital stripe; postmedial band curved slightly basad near costa; band colour pale whitish buff; fringe usually entirely or predominantly whitish buff, occasionally dark near wing apices; basal ⅔ of costa pale, anal margin finely lined in pale; anal dash usually present; basal half of cubital vein usually pale-lined; underside similar to upperside, but bands less contrasting and colours paler; sexes similar. Hindwing - Ground colour pale yellowish white in males, females yellow, rarely entirely black; markings dark brown to black, well developed, postmedial and subterminal markings usually confluent; antemedial markings well developed, often expanded to broad band along anal margin confluent with distal margin band; female markings usually discrete, not forming confluent bands; ventrally with similar pattern and duller ground colour. ***Male genitalia*** - Distal portion of valve gradually tapering to slightly pointed apex, apex directed somewhat caudo-ventrally; saccular extension poorly developed, saccular process poorly developed; uncus broad-based, process evenly tapered to point; juxta 2x wider than long; aedeagus with dorsad curve at ⅔ distance beyond base; distal chamber of vesica nearly globose, scobinate, spinules relatively large; medial chamber roughly as wide as distal chamber; most similar to *G. williamsii*. ***Female genitalia*** - Ductus bursae unsclerotized; corpus bursae pear-shaped to globose and relatively small, 3x width of ostium bursa; signa rounded or slightly oblong, relatively small (2.3×10^{-1} mm); posterior apophysis 1.5x longer than length of papillae anales.

Immature stages: the following is based on the brief description given by Kimmich (1966). Egg spherical, pale yellow; mature larva with black head and integument, tubercles black, finely spotted with white; setae short, black dorsally, maroon laterally; dorsal line continuous, dotted or absent, ranging in colour from white to ochre or brown; pupa pruinose, head bristled.

Biology

Adult collection dates range from mid May to late August, peaking in mid to late July. This rarely collected species inhabits dry, montane and subalpine meadows, most commonly occurring near or above treeline. Most specimens have been collected by day, but they are also attracted to light. Males fly in late afternoon (L. Crabo, pers. comm.). The only recorded larval host is *Claytonia lanceolata* Pursh. (Portulacaceae), although the larvae undoubtedly feed on other plants as well. Eggs are laid loosely in batches of up to about 200 (Kimmich 1966).

Distribution

Southwestern British Columbia and west central Alberta south to Montana and Washington (Fig. 2-121). Also occurs in northeastern Oregon according to Ferguson *et al.* (2000).

Molecular Variation

Four specimens of *elongata* from three localities exhibited three haplotypes, two of which were similar or indentical to *G. complicata* haplotypes in the Western lineage (CP1, EL1; Fig. 2-133). The third haplotype from an Alberta specimen was of the Eastern lineage (Fig. 2-134), and was shared with *G. williamsii, G. virguncula* and *G. margo* (Fig. 2-134).

Remarks

Although considered a subspecies of *G. williamsii* at one time, there are numerous subtle but distinct morphological and phenotypical differences. The two species occur together at Hailstone Butte, Alberta, and are broadly sympatric in the Alberta Rocky Mountain front ranges.

GRAMMIA YAVAPAI NEW SPECIES

FIGS. 2-30, 2-64, 2-122.

Type Material

Holotype - ♂. **Arizona,** Coconino Co., Parks, 27 June 1957, L.M. Martin, R.J. Ford, W.A. Rees [LACM]. ***Paratypes*** - 5♂♂ 1♀. Same data as holotype, 1♂ [LACM]; Same data as holotype, 26 June 1957 3♂♂ [LACM, CNC]; Arizona, Coconino Co., T23N R7E, Sec. 23, Sugarloaf Mtn., 8480', 3 July 1987, Eric H. Metzler, UV, 1♂ [CNC]; Arizona, Coconino Co., Williams, [no date, reared ex pupa] 1♀ [USNM].

Etymology

Grammia yavapai is named after the indigenous tribe of central Arizona. The name is used as a noun in apposition.

Diagnosis

This species resembles *G. williamsii* in overall size and wing pattern. Males can easily be distinguished from *G. williamsii* by the much longer antennal branches, nearly twice as long in *G. yavapai* (5x longer than length of segments, vs. 2.5 - 3x in *G. williamsii*), pale antennal scaling, and the smaller eyes. Both sexes can be recognized by the curved postmedial line (straight or nearly so in *G. williamsii*), one or more transverse bands extending beyond postcubital stripe, and yellowish to yellowish-pink hindwing. The two species are not known to occur together, as *G. yavapai* occurs to the south of *G. williamsii's* range.

Although superficially most similar to *G. williamsii*, the long antennal pectinations, buff antennal scaling and reduced eyes suggest a closer affinity to *G. blakei* (from which it differs by the larger size, broader forewing shape, less developed forewing bands, longer antennal branches). *Grammai yavapai* may be endemic to north-central Arizona.

Description

Head - Vestiture of frons and vertex pale buff, vertex varying to pale buff and dark brown centrally; eyes slightly reduced, diameter averaging 6.3 x 10^{-1} mm (n = 5 males); male antennae strongly bipectinate, pectinations averaging 7.6 x 10^{-1} mm, 4.9 times longer than intersegmental distance (n = 5); antennal scales predominantly pale buff, with scattered dark brown scales; female antennae strongly biserrate. ***Thorax*** - Vestiture dark brown with broad, pale buff borders on vertex, patagia and tegulae; predominantly pale buff ventrally, dark brown laterally; legs pale buff and dark brown, predominantly dark brown in female; yellowish buff central tuft at base of forecoxae. ***Abdomen*** - Dorsal ground colour dull yellowish buff in males, female brighter yellow, pale buff near apex; medial and lateral markings dark brown, medial markings confluent into solid, even-edged band; males pale buff ventrally with highly reduced dark brown lateral spots; female entirely dark brown ventrally with pale segment borders. ***Forewing*** - Mean forewing length 14.4 mm (n = 5); ground colour chocolate brown (perhaps faded somewhat due to age of specimens); basal and antemedial band absent, or present as indistinct pale costal bar; antemedial also sometimes evident as short line below postcubital stripe; medial band well-developed, often slightly wider than postmedial and subterminal bands, curved, extending slightly below postcubital; postmedial band well developed, curved basad near M_3, often extending slightly beyond postcubital; subterminal band well developed; bands pale buff in colour; fringe dark brown and pale buff; costa with narrow, pale buff scales extending ½ to ¾ of distance to apex; anal margin pale, anal dash absent; underside similar to upperside, but bands less contrasting; sexes similar. Hindwing - Ground colour pinkish-yellow to dull yellow, deeper saturated yellow in female; markings dark brown, well developed and often confluent, antemedial markings streaked disto-basad; ventrally with similar pattern and duller ground colour; female with more reduced hindwing spots. ***Male genitalia*** - Distal portion of valve gradually tapering to rounded apex; saccular extension reduced, saccular process well-developed; uncus broad-based, process evenly tapered to point, 3x longer than width of base; juxta slightly wider than long; aedeagus with dorsad curve at ⅔ distance beyond base; distal chamber of vesica relatively small, broad, and slightly kidney-shaped, coarsely scobinate; medial chamber ½ width of distal chamber; vesica slightly longer than aedeagus, diverticuli indistinct. ***Female genitalia*** - Not examined.

Biology

Adult collection dates range from late June to early July. The reduced eyes suggest this species may be partially diurnal, but males have also been collected at light. The only known female specimen was reared.

Distribution

Known only from the San Francisco volcanic field in Coconino County, Arizona (Fig. 2-122).

Molecular Variation

Not examined.

GRAMMIA BOWMANI FERGUSON AND SCHMIDT

FIGS. 2-26, 2-61, 2-119.

Grammia bowmani Ferguson and Schmidt, 2007: 44.

Type Material

Holotype male from Colorado, Mesa Co., Coal Mine Pt., Black Ridge, 7,000 ft., 16 May 1987, D.E. Bowman [USNM, not examined; topotypes and paratypes examined]; Paratypes (51 males; CSU, USNM, AMNH, CNC, CU, RBCM, UCB and D. Bowman personal collection), same locality and collector as holotype, 16 May 1987 (5 males), 18 May 1985 (1 male), 26 July 1975 (3 males); 11 males, Upper Red Canyon, Colorado National Monument, Mesa Co., 31 May 1997, B. Rodgers family; 1 male, West Entrance, 4,700 ft., Colorado National Monument, Mesa Co., 1 June 1996, B. Rodgers family; 3

males, Upper No Thoroughfare Canyon, 6,200 ft., Colorado National Monument, Mesa Co., 18 June 1996, B. Rodgers family; 20 males, same locality and collectors, 12 July 1997. 1 male, Mesa Co., Colorado National Monument, Upper Ute Canyon, 7 June 2000, Opler and Slossen; 1 male, Mesa Co., Colorado National Monument, head of Red Canyon, 3-4 July 2000, J. Moore; 5 males, Utah, San Juan Co., Blanding, 1 July 1970, R. Carcasson.

Diagnosis

The size, wing pattern and coloration of *bowmani* are most similar to *G. williamsii* and dark forms of *G. nevadensis*. It can be distinguished from *G. nevadensis* by the shorter antennal branches (longest branches 3 - 3.5 x intersegmental distance versus 4 - 4.5 x), smaller male juxta (1 mm wide or less, versus greater than 1 mm), and shorter, more globose male vesica. The forewing medial and postmedial bands tend to be straight or nearly so, not curving basad near the costa as in *G. nevadensis*. Wing fringes entirely or predominantly black, not predominantly white as in *G. nevadensis*, and the vestiture of the forecoxae is pale brown to dull yellow, while bright yellow in *G. nevadensis*. Compared to *G. williamsii*, *G. bowmani* has longer antennal branches (3 – 3.5 x intersegmental distance versus 2.5 x), and the medial and/or postmedial lines are better developed, extending toward the anal margin beyond the postcubital stripe, very rarely so (<5%) in *williamsii*. Vestiture of legs and thorax underside dark brown, with buff area restricted to forecoxae, compared to extensive buff thorax underside in *williamsii*.

Description

Head - Frons, vertex and palps dark brown to black, palpi and frons occasionally with a few pale scales; eyes fully developed; male antennae moderately bipectinate, pectinations averaging 5.98×10^{-1} mm, 3.5 times longer than intersegmental distance (n = 3); antenna with dark brown dorsal scales, scattered buff scales. ***Thorax*** - Vestiture entirely dark brown to black, or with typical pale buff borders on vertex, patagia and tegula; entirely dark brown ventrally, tuft of scales between coxae reduced or absent, pale buff, rarely yellow, when present; legs entirely dark brown or dark brown and yellowish buff. ***Abdomen*** - Ground colour pink, medial and lateral markings dark brown to black;

black ventrally, with thin, pale buff border along distal margin of segments. ***Forewing*** - Mean forewing length 14.8 mm for males ($n = 49$); ground colour dark brown to black, fringe entirely black or black with small areas of buff; bands pale buff, antemedial band incomplete or absent, although a fragment of the antemedial or postmedial or both may extend toward inner margin beyond postcubital stripe, but usually not reaching inner margin; medial and postmedial bands nearly straight, as in *G. williamsii,* not curving basad near costa as in *nevadensis*; similar ventrally, with colours more washed out. Hindwing - Ground colour rose to pale pink, patterned with black; antemedial and medial markings usually present, the latter often developed into streaks; postmedial spots well developed; postmedial and subterminal markings usually confluent; fringes black often buff at anal angle; ventral and dorsal pattern simlar, colours less bright ventrally. ***Male genitalia*** - Distal portion of valve on average narrower than in *G. nevadensis*; saccular process well-developed, saccular extension moderately developed; uncus long evenly tapered, typical of genus; juxta relatively narrow for members of this group, about ⅗ as wide as that of *nevadensis*; aedeagus relatively broad, distal end curving dorsally, and opening to the right as in other *Grammia*; vesica with broad, nearly globose distal chamber, about ⅖ as large as that of *nevadensis*, scobinate zone on distal chamber less extensive than in *nevadensis,* spinules relatively large, more so than in *nevadensis*, similar to *williamsii*; distal chamber smaller and medial chamber broader than in *nevadensis*, closely resembling *williamsii.*

Female: unknown.

Biology

Adult dates of capture span dates from mid May to late July. *Grammia bowmani* occurs at elevations of 5000 - 7000 feet. The female is not known, and is likely not attracted to light, as is the case for other species in the *nevadensis* group. The immature stages are unknown.

Distribution

Known from western Colorado and southeastern Utah (Fig. 2-119).

Molecular Variation

Two specimens of *G. bowmani* from a single site exhibited two haplotypes of the Western lineage, differing by a single base pair (Table 2-2, Fig. 2-133); one haplotype was shared with *G. williamsii* (Fig. 2-133).

Remarks

Although this species was discovered only recently, it can be quite common where found. It flies with *G. incorrupta* in Mesa County, Colorado.

GRAMMIA BLAKEI (GROTE)

FIGS. 2-32, 2-66, 2-91, 2-124.

Apantesis blakei Grote, 1864: 523, pl. 5, fig. 2; Franclemont, 1983: 117.
Grammia blakei (Grote); Ferguson and Opler 2006: 10.

Type Material

Described from a single female, type number 7684 [ANSP, not examined]. The type locality is "Colorado Territory" [Colorado, USA].

Diagnosis

Grammia blakei somewhat resembles small, pale *G. nevadensis* or *G. williamsii*, but the pale whitish-buff antennae and presence of a forewing basal dash along the anal vein will almost invariably distinguish *G. blakei* specimens. Internally, the male vesica is unusually distinctive; the basal chamber is relatively large, and the distal chamber is smaller than the medial chamber (larger than or equal to medial chamber in other *G. nevadensis* group species). *Grammia blakei* flies relatively early in the spring (occasionally with a second, late summer flight), overlapping partially with the start of the flight of *G. williamsii* in the northern Great Plains, while sympatric *G. nevadensis* populations do not fly until late summer/early fall.

Description

Head - vestiture of palps and frons pale buff, vertex black, pale buff laterally; eyes reduced mean maximum diameter 5.68 x10^{-1} mm (n = 6 males), gena exposed adjacent to lateral eye margin; male antennae strongly bipectinate, pectinations averaging 5.75 x 10^{-1} mm, 3.9 times longer than intersegmental distance (n = 6); dorsal scales of antenna predominantly pale buff; female antennae strongly biserrate to slighty bipectinate. ***Thorax*** - Vestiture black with broad, pale buff borders on vertex, patagia and tegulae; black thorax form absent; pale buff ventrally, central tuft yellowish buff, black laterally; legs predominantly pale buff, coxa and tibia pale buff and black. ***Abdomen*** - Dorsal ground colour pale yellow to yellowish orange, pale buff near apex; medial and lateral markings black; pale buff ventrally, lateral black markings often reduced in males, expanded in females and often converging laterally into broad black band. ***Forewing*** - Mean forewing length 13.8 mm (n = 6 males); ground colour dark chocolate brown to black; banding pattern pale buff, moderately developed; basal band extending to postcubital or reduced to costal wedge, antemedial band usually present, most often as costal wedge and band below postcubital; medial band well-developed, extending caudally beyond postcubital; postmedial band well developed, curving slightly basad near costa; subterminal band well-developed; anal dash usually present; cubital vein sometimes pale-lined near postcubital stripe, especially in females; fringe entirely pale buff, or with dark scales near tornus; basal 7/8 of costa lined pale buff; sexes similar. Hindwing - Ground colour pale yellow, rarely orange, brighter in females; markings well developed, dark brown to black; antemedial spot near anal margin usually streaked basad; medial spot prominent, postmedial and subterminal spots prominent and often confluent; females with relatively reduced markings; ventrally with similar pattern and duller ground colour. ***Male genitalia*** - Distal portion of valve gradually tapering to rounded apex; saccular extension and saccular process moderately developed; uncus broad-based, process evenly tapered to point; juxta wider than long; aedeagus with dorsad curve at ⅗ distance beyond base; vesica with relatively large basal chamber, medial and distal chamber small and equal in size, equally scobinate, spinules relatively large. ***Female genitalia*** - Ductus bursae unsclerotized; basal half of ductus bursae widened considerably, about half the diameter of corpus bursa; corpus bursae more or less globose and relatively small, 2x width of ostium bursa; signum 1 rounded-triangular in shape, larger than signa 2-4; signa coarsely scobinate; appendix bursae with broad, angled elbow, not evenly tapered; posterior apophysis slightly longer than length of papillae anales.

Biology

Adult collection dates range from late May to early September, and in some years there is a partial second generation in the southern parts of the range (Ferguson, cited as *in lit.* in Byers 1988). In the northern Great Plains, the species is univoltine, the larvae aestivating in mid summer, feeding again in fall, then diapausing (Byers 1988). Peak flight activity is from late May to early June, with a few Montana records for August. Kansas records are for mid July to early September. *Grammia blakei* is primarily a low-elevation, Great Plains grassland species, and can be abundant in sparsely vegetated, sandy prairie, including overgrazed native pastures (Byers 1988). It also occurs at higher elevations, with records from 9200' in Colorado and 6500' (near treeline) in southwestern Alberta. Adults are primarily diurnal, and rarely come to light (Byers 1988; Schmidt, unpubl. data). Males are active in late afternoon (Schmidt, unpubl. data), and mating occurs during the first hour of darkness (Byers 1988). Byers (1989) described trapping techniques using virgin females, and males apparently approach calling females by crawling, since traps that were not placed directly on the ground caught few or no males. Larvae feed on *Antennaria dimorpha* (Asteraceae), *Koeleria cristata, Poa sandbergii, Stipa comata, Agropyron smithii, Eurotia lanata, Bouteloua gracilis* (Poaceae), and *Carex* spp. (Cyperaceae), and in captivity will also accept a variety of monocot and dicot crop plants (Byers 1988). Larvae are occasionally abundant enough to cause significant damage to spring wheat, reaching numbers of up to 100 larvae / m^2 (Byers 1988).

Distribution

Occurs from the southern prairie provinces south to Texas, and west Colorado (Fig. 2-124) . Essentially a Great Plains species and contrary to Byers (1988), it is not known from southern British Columbia and California. Ferguson *et al.* (2000) record it as far south as Arizona and New Mexico.

Molecular Variation

Two specimens from a single locality exhibited the same haplotype in the Western lineage, shared with *G. williamsii* (Fig. 2-133). Both samples sharing this haplotype originated from adjacent prairie sites in southeastern Alberta (Appendix 2-1).

Remarks

Despite the historical misapplication of the name *blakei* to both *G. williamsii* and *G. nevadensis*, and the *cox1* haplotypes shared with *G. williamsii*, there are clear morphological and ecological differences between all three species; these three species often occur in strict sympatry, *G. blakei* and *G. williamsii* often flying at the same time.

GRAMMIA CERVINOIDES (STRECKER)

FIGS. 2-33, 2-67, 2-125.

Arctia cervinoides Strecker, 1876: 151.
Apantesis cervinoides (Strecker); Franclemont 1983: 117.
Grammia cervinoides (Strecker); Ferguson and Opler 2006: 10.

Type Material

Male holotype from Mt. Flora, [Clear Creek County], Colorado, [USA]. [FMNH, photograph examined].

Diagnosis

This day-active species of the alpine zone in the Colorado Rocky Mountains is not likely to be confused with other *Grammia* species. The small size, reduced eyes, whitish and grey hindwings, and presence of most of the forewing bands are unique.

Description

Head **-** vestiture of palps and frons pale buff or dark brown, vertex entirely black, or black and pale buff laterally; eyes reduced, mean maximum diameter 4.33×10^{-1} mm (*n* = 3 males), gena exposed adjacent to lateral eye margin; male antennae moderately bipectinate, pectinations averaging 2.82×10^{-1} mm, 1.9 times longer than intersegmental distance (*n* = 3); dorsal scales of antenna predominantly dark brown, with scattered buff scales. ***Thorax*** - Vestiture black to dark brown with pale buff borders on vertex, patagia and tegulae; black thorax form absent; pale buff ventrally, central tuft reduced, pale buff; legs predominantly pale buff, coxa and femur dark brown. ***Abdomen*** - Dorsal ground colour dull, pale buff, black medial band wide; lateral markings black; pale buff ventrally, lateral black markings black. ***Forewing*** - Mean forewing length 11.9 mm (*n* = 3 males); ground colour dark greyish-brown to black; banding pattern pale buff, moderately developed, bands relatively broad; basal band absent or reduced to costal wedge, antemedial band usually present, extending to postcubital stripe or beyond; medial band well-developed, usually extending caudally beyond postcubital; postmedial band well developed, nearly straight or curving slightly basad near costa; slightly angled at vein M_3; subterminal band well-developed; anal dash usually present; cubital vein not pale lined; fringe variable, pale buff, dark brown or combination thereof; costa usually finely lined whitish buff; anal margin whitish buff. Veins rarely (two of 15 specimens) white-lined according to Smith (1938a); sexes similar. Hindwing - Ground colour dull whitish buff, often with dusky cast; markings well developed, dark brownish grey, often suffused and with borders indistinct; antemedial spots often streaked basad; medial spot prominent, postmedial and subterminal spots prominent and often confluent; ventrally with similar pattern, overall paler. ***Male genitalia*** - Distal portion of valve gradually tapering to rounded apex; saccular extension and saccular process reduced; uncus broad-based, process evenly tapered to point; juxta 1.5x wider than long; aedeagus with dorsad curve at ⅔ distance beyond base; vesica with relatively small basal, medial and distal chambers; medial and pical chambers coarsely scobinate, spinules relatively large; distal chamber broadly kidney-shaped, resembling *nevadensis* in this respect. ***Female genitalia*** - not examined.

Biology

Adults are diurnal, and occur in alpine habitat, including rocky slopes. Collection dates are from early to mid July.

Distribution

Occurs above treeline in the Rocky Mountains of Colorado (Fig. 2-125).

Molecular Variation

Not examined.

Remarks

Grammia cervinoides is the smallest species of *Grammia*, although small *G. quenseli* specimens are similar in size. This species has traditionally been treated as being closely related to *G. quenseli*, due the superficial resemblance in the dusky colouration, small size and occasional expression of forewing vein lines. The extent of the forewing banding pattern, broad hindwing shape and the molecular data all suggest a closer relationship to the *nevadensis* group. The name *cervinoides* means "like *cervini*", referring to another dusky grey, high alpine arctiine, *Holoarctia cervini* of the European Alps.

GRAMMIA ORNATA (PACKARD)

FIGS. 2-36, 2-69, 2-93, 2-127.

Callarctia ornata, 1864; Proc. ent. Soc. Philad. 3: 115
Arctia achaia Grote and Robinson, 1868; Trans. Am. ent. Soc., 1: 334
Apantesis ornata ab. *ochracea* Stretch, 1872; Illust. Zygaenidae Bombycidae N. Am. 1: 125, pl. 5, f. 21
Arctia simplicior Butler, 1881; Ann. Mag. Nat. Hist. (5) 8: 311
Arctia achaia var. *barda* Hy. Edwards, 1881; Papilio 1: 39
Euprepia (Cymbalophora) blakei var. *perpicta* Dyar, 1893; Psyche 6: 381

Arctia achaia var. *maculosa* Stretch, 1906 J. N.Y. Ent. Soc 120 pl. 6 figs. 3,4

Arctia achaia var. *rivulosa* Stretc Packard h, 1906 J. N.Y. Ent. Soc 121 pl. 6 figs. 8,9

Arctia achaia var. *ochracea-rivulosa* Stretch, 1906 J. N.Y. Ent. Soc 121 pl. 6 fig. 10 [Note: this name should be emended to *ochracearivulosa* in accordance with Article 45.6 of the code (ICZN, 1999)]

Apantesis californica Cassino, 1917. Lepidopterist 1:100; plate opposite pg. 102

Apantesis ornata ab. *sulphuricella* Strand, 1919; Lepidopterorum Catalogus, 22: 416

Apantesis ornata (Packard); Franclemont 1983: 117.

Grammia ornata (Packard); Ferguson and Opler 2006: 10.

Type Material

Callarctia ornata: described from an unstated number of males; according to Smith (1938a), a male holotype and paratype are in the MCZ [not examined]. The type locality is San Mateo, [San Mateo Co.], Cal[ifornia, USA].

Arctia v. *achaia*: described from a male and female syntype, the female syntype, from the Sierra Nevada, California, is in the AMNH according to Smith (1938a) [not examined].

Apantesis ornata ab. *ochracea*: Described from an unstated number of specimens; type material lost or destroyed. The type locality is not explicitly stated, although Stretch (1872) describes it as being "widely distributed over California."

Arctia simplicior: holotype female in the BMNH according to Smith (1938a) [not examined]. The type locality is Jacksonville, [Tuolumne Co.,] California, [USA].

Arctia achaia var. *barda*: Described from two syntypes, one from North[ern] Calif[ornia] and [The] Dalles, Oregon, in the AMNH according to Smith (1938a) [not examined].

Euprepia blakei var. *perpicta*: Female holotype in USNM according to Smith (1938a) [not examined]. The type locality is Yosemite, [Mariposa Co.], California, [USA].

Arctia achaia var. *maculosa, rivulosa, ochracea-rivulosa*: Based on the illustrations given in the orlginal description. No written description or indication of the type material or locality is provided. Types presumed lost.

Apantesis californica: female holotype from Eldredge [=Eldridge, Sonoma Co.?], California, [USA] in the USNM according to Smith (1938a) [not examined].

Apantesis ornata ab. *sulphuricella*: based on an aberrant specimen, and is therefore an unavailable infrasubspecific name.

Diagnosis

The lined forewing veins and large size will distinguish most specimens of *G. ornata* from most other western *Grammia*, with the exception of the much smaller *G. edwardsii*, distinguished by the pale basal third of the antennae (dark in *ornata*) and additional characters given in the *G. edwardsii* account. *Grammia hewletti* is most similar to *G. ornata*, but is restricted to southernmost California; diagnostic characters segragating these two species are given in the *G. hewletti* diagnosis.

Forms of *G. ornata* with unlined forewings are common in many populations, and these can be distinguished from most other *G. nevadensis* group species by the presence of antemedial hindwing spots, yellow to scarlet hindwing colour (never pinkish), entirely pale vertex of the head (very rarely with black, almost always black with pale in other species), broader wing shape and spring flight season. Throughout most of its range, *G. ornata* is the only *Grammia* that flies in spring. Internally, most male *G. ornata* can be distinguished by the well-defined triangular or elongate saccular extension, which is weakly defined or absent in other *Grammia*.

Description

Head - vestiture of palps black, frons and vertex entirely pale to yellowish or pinkish buff, vertex very rarely black centrally; eyes well developed mean maximum diameter 9.2×10^{-1} mm (n = 6 males); male antennae strongly bipectinate, pectinations averaging 5.5×10^{-1} mm, 3.1 times longer than intersegmental distance (n = 6); dorsal scales of antenna black, occasionally with scattered pale buff scales; female antennae strongly biserrate to slightly bipectinate. ***Thorax*** - Vestiture of vertex, patagia and tegulae black with broad, pale, yellowish or pinkish buff borders; patagia occasionally entirely pale, black thorax form absent; black ventrally, central tuft yellow, sides black; legs predominantly black, tibia pale buff laterally. ***Abdomen*** - Dorsal ground colour yellow to orange-yellow, pale buff near apex; medial and lateral markings black, medial band relatively broad; pale whitish-buff ventrally, lateral black markings well developed but not confluent in males; females usually entirely black dorsally. ***Forewing*** - Mean forewing length 18.6 mm ($n = 6$ males); ground colour black; banding pattern pale, yellowish or pinkish buff, variably developed; basal band usually reduced to costal wedge; antemedial band usually present, often broader than other bands; medial band well-developed; postmedial band well developed, generally not curving but with distinct angle at M_3; vein lines variably developed, extending to distal margin or absent entirely; fringe entirely pale buff; costa entirely pale, or pale areas restricted to where bands meet costa; anal margin pale-lined; ventrally with colours paler, and more yellowish cast; sexes similar. Hindwing - Ground colour pale to bright yellow, orange or scarlet; markings well developed, black; antemedial spots discrete, streaked basad or completely confluent basally with black basal markings; medial spots usually well-developed, posterior medial spot sometimes suffused basally; postmedial and subterminal spots prominent, confluent in northern populations; ventrally with similar pattern and duller ground colour; sexes similar. ***Male genitalia*** - Distal portion of valve gradually tapering, apex slightly curved ventrocaudally; saccular extension strongly to moderately developed, saccular process moderately developed; uncus broad-based, process evenly tapered to point; juxta 2x wider than long; aedeagus with dorsad curve at ⅔ distance beyond base; vesica with relatively small basal chamber, length twice that of medial chamber width, scobinate, spinules relatively large; medial chamber finely scobinate. ***Female genitalia*** - Ductus bursae unsclerotized; basal half of ductus bursae widened, 1/3 diameter of corpus bursa; corpus bursae pear-shaped, relatively large, 4x width of ostium bursa; signa round to slightly oblong, approximately equal in size (3.00×10^{-1} mm); signa coarsely scobinate; appendix bursae evenly coiled; posterior apophysis slightly longer than length of papillae anales.

Biology

Grammia ornata is one of the few species of the genus that fly in spring, and most adult collection dates are from mid May to late June. Two examined specimens, one each from August and September (central and northern WA) may indicate a partial second generation. Both sexes come to light, although females are rarely collected. This species inhabits a relatively wide range of habitats, but prefers open woodland, and is absent from the drier, low elevations of the Great Basin.

Distribution

Southern British Columbia south through the Pacific Northwest to southern California, northern Utah, and western Wyoming/Montana (Fig. 2-127).

Molecular Variation

G. ornata, like *G. nevadensis*, exhibits large intraspecific sequence divergences and is paraphyletic with respect to other species in the *nevadensis* group. Nine specimens from eight localities all represented unique haplotypes, with a maximum of 4.0% intraspecific divergence (Table 2-2). Three clusters were evident, largely corresponding to geographic regions. The first cluster consisted of southern Oregon samples, both coastal and southwestern (OR2,3,4; Fig. 2-133); the second lineage consisted of northeastern California and southeastern British Columbia samples, and also included one southwestern Oregon sample (OR5,6,7,8; Fig. 2-133). Two southern BC samples (CP1, OR1) grouped with *G. complicata,* and haplotype CP1 was shared among *G. ornata, G. complicata* and *G. elongata* (Fig. 2-133), originating from southwestern BC (Appendix 2-1).

Remarks

Grammia ornata is the most variable *Grammia* in terms of forewing pattern and hindwing colour, and the large number of synonyms is testament to this. Specimens from the northern parts of the range (southern BC, northern ID and WA) are smaller with more extensive hindwing dark markings compared to those from northern CA and southern OR, and are also most variable in development of the forewing vein lines. Of about 80 BC specimens, 50% have fully developed vein lines and 50% have vein lines partially devloped or absent. Great Basin populations usually exhibit the lined form, while populations in the Siskiyou Mountains and adjacent regions (Josephine County, OR; Trinity, Siskiyou, Modoc, Mendocino Counties, CA) usually lack vein lines.

The taxa *G. hewletti* and *G. complicata* have both been treated as species separate from *G. ornata* or as subspecies, but as discussed under *G. hewletti* and *G. complicata*, I retain both as separate species.

GRAMMIA HEWLETTI (BARNES AND MCDUNNOUGH), REVISED STATUS

FIGS. 2-37, 2-71, 2-94, 2-129.

Apantesis ornata hewletti Barnes and McDunnough, 1918 pl. 13 figs. 3,4
Apantesis hewletti (Barnes and McDunnough); Franclemont 1983: 117.
Grammia ornata (=*hewletti* Barnes and McDunnough); Ferguson & Opler 2006: 10.

Type Material

Described from an unstated number of specimens, consisting of at least one male and one female syntype; the male syntype matching the photo in the original description is in the USNM [examined], labelled "A. ornata/ v. hewletti/ Type ♂/ B and McD", "Nellie/ ~~S. Bern. Co.~~/ Calif." [S. Bern. Co. crossed out], "Photograph/ Pl. 13 No. 3", "♂ genit./ on slide/ Aug. 31, 1937/ M.E.S. #1501".

Diagnosis

Grammia hewletti is slightly larger and more brightly coloured than *G. ornata*, and nearly always has the forewing basal band well developed (rare in *G. ornata,* absent in *G. complicata*). The hindwing spots are smaller, never confluent as in *G. complicata* and northern *G. ornata*. Internally, the base of the uncus has two broad, flat and rounded lateral flanges, a character unique among *Grammia*. the distal portion of valve is broad and rounded, not tapering gradually, and the saccullus is more pronounced than in most other *Grammia*. See also 'Remarks' below.

Description

Head - vestiture of palps black, frons and vertex entirely pale to yellowish buff, vertex very rarely black centrally; eyes well developed, mean maximum diameter 1.10 mm (n = 4 males); male antennae strongly bipectinate, pectinations averaging 7.6 x 10^{-1}

mm, 4.3 times longer than intersegmental distance (*n* = 4); dorsal scales of antenna black, occasionally with scattered pale buff scales; female antennae strongly biserrate. ***Thorax*** - Vestiture of vertex, patagia and tegulae black with broad, pale, yellowish or pinkish buff borders; patagia occasionally entirely pale, black thorax form absent; black ventrally, central tuft yellow, sides black; legs predominantly black, tibia pale buff laterally. ***Abdomen*** - Dorsal ground colour yellow to orange-yellow, pale buff near apex; medial and lateral markings black, medial band relatively broad; pale whitish-buff ventrally, lateral black markings well developed but not confluent in males; females usually entirely black dorsally. ***Forewing*** - Mean forewing length 20.0 mm (*n* = 2 males); ground colour black; banding pattern pale, yellowish or pinkish buff, variably developed; basal band usually extending to postcubital; antemedial band often broader than other bands; medial band well-developed; postmedial band well developed, generally not curving but with distinct angle at M_3; vein lines variably developed, extending to distal margin or absent entirely; fringe entirely pale buff; costa entirely pale, or pale areas restricted to where bands meet costa; anal margin pale-lined; ventrally with colours paler, and more yellowish cast; sexes similar. Hindwing - Ground colour usually bright yellow, varying to orange or scarlet; markings well developed, black; antemedial spots discrete, often reduced; medial spots usually well-developed, posterior medial spot sometimes suffused basally; postmedial and subterminal spots prominent; ventrally with similar pattern and duller ground colour; sexes similar. ***Male genitalia*** - Distal portion of valve broad, not tapered, apex broad and rounded; saccular extension strongly developed, saccular process moderately developed; uncus broad-based, process evenly tapered to point, base of uncus with broad, rounded flanges; juxta 2x wider than long; aedeagus with dorsad curve at ⅔ distance beyond base; distal chamber twice length of medial chamber width, scobinate, spinules relatively large; medial chamber finely scobinate. ***Female genitalia*** - Ductus bursae unsclerotized; basal half of ductus bursae widened, 1/3 diameter of corpus bursa; corpus bursae pear-shaped, relatively large, 4x width of ostium bursa; signa round to slightly oblong, relatively small; signa coarsely scobinate; appendix bursae evenly coiled; posterior apophysis slightly longer than length of papillae anales.

Biology

Adult capture dates are for May. Nothing is known of the immature stages, although Barnes and McDunnough (1918) remarked that the larvae match those of *G. ornata*.

Distribution

Southwestern California (Fig. 2-129).

Molecular Variation

Not examined.

Remarks

Although *G. hewletti* was originally described as a subspecies of *G. ornata*, Smith (1938a) raised it to species, based on the wing marking characters mentioned above, and the absence of the saccular extension of the male valve. Although the valve process is sometimes absent in *G. ornata*, other unique characters listed in the diagnosis suggest *G. hewletti* is best segregated as a separate species. This is one of the few instances within the genus where pronounced male genitalic differences occur between closely related taxa. There is no indication of clinal variation in male genitalic morphology north of the San Diego area *G. hewletti* populations, with an abrupt change to typical *G. ornata* morphotypes in Ventura and Kern counties, California.

GRAMMIA COMPLICATA (WALKER)

FIGS. 2-38, 2-70, 2-95, 2-128.

Arctia quenselii ab. *complicata* Walker, 1864 [1865]: 279.
Apantesis ornata complicata Franclemont, 1983: 117.
Grammia complicata Ferguson and Opler 2006: 10.

Type Material

Male holotype in BMNH [not examined]. The type locality is Vancouver Island, [British Columbia, Canada].

Diagnosis

Grammia complicata is distinguished from *G. ornata* by the much smaller eyes, pale hindwing ground colour, extensive suffused hindwing markings, reduction of forewing bands, smaller more elongate forewings, and absence of the unlined forewing form. Internally, most male specimens of *G. complicata* differ from those of *G. ornata* by the absence of the saccular extension. The reduced eye size suggests *G. complicata* may be active during the day, unlike *G. ornata*. See also 'Remarks', below

Description

Head - vestiture of palps black with pale buff apex; frons and vertex entirely pale buff, vertex varying to black with pale buff laterally; eyes reduced, gena exposed at lateral eye margin, mean maximum eye diameter 6.04 x10^{-1} mm (*n* = 10 males); male antennae strongly bipectinate, pectinations averaging 4.43 x 10^{-1} mm, 2.9 times longer than intersegmental distance (*n* = 10); dorsal scales of antenna black with scattered pale buff scales; female antennae strongly biserrate. ***Thorax*** - Vestiture of vertex, patagia and tegulae black with broad, pale buff borders; black thorax form absent; black ventrally, central tuft yellow, sides black; legs predominantly pale buff. ***Abdomen*** - Dorsal ground colour pale yellow to orange-yellow, pale buff near apex; medial and lateral markings black, medial band relatively broad; pale whitish-buff ventrally, lateral black markings broad but not confluent in males; females entirely black dorsally. ***Forewing*** - Mean forewing length 15.7 mm (*n* = 6 males); ground colour black; banding pattern pale buff to yellowish-ochre; basal band absent, antemedial band usually absent; medial band reduced or absent; postmedial band well developed, generally not curving but with distinct angle at M_3; vein lines variably developed, usually extending to distal margin, sometimes reduced but never absent; fringe entirely pale buff, rarely with some dark scales; costa entirely pale, or pale areas restricted to where bands meet costa; anal margin pale-lined; ventrally with colours paler, and more yellowish cast; sexes similar. Hindwing

- Ground colour usually pale whitish yellow, varying to yellow or rarely yellowish orange; markings well developed, black, extensively confluent; anal margin and basal area often entirely black; ventrally with similar pattern and duller ground colour; sexes similar. ***Male genitalia*** - Distal portion of valve gradually tapering, apex rounded, directed slightly caudoventrally; saccular extension and saccular process moderately developed; uncus broad-based, process evenly tapered to point; juxta slightly wider than long; aedeagus with dorsad curve at ⅗ distance beyond base; vesica with relatively small basal chamber, length twice that of medial chamber width, scobinate, spinules relatively large; medial chamber finely scobinate. ***Female genitalia*** - Ductus bursae unsclerotized; corpus bursae pear-shaped, relatively small, 4x width of ostium bursa; signa small, rounded; signa coarsely scobinate, spines few; appendix bursae evenly coiled; posterior apophysis equal in length to papillae anales.

Biology

Occurs in dry Garry Oak meadows and sandy beach habitats. Adult dates of capture are primarily from late May to mid June. Although specimens are occasionally collected at light, the reduced eye size suggests that this is a day-active species.

Distribution

Known only from southeastern Vancouver Island and several of the Gulf Islands of British Columbia, and Pacific Co., Washington (Fig. 2-128).

Molecular Variation

Four samples of *G. complicata* from four localities exhibited three haplotypes, differing by a maximum of 0.85% (Table 2-2). Haploptye CP1 was shared among *G. complicata, G. ornata* and *G. elongata*.

Remarks

Grammia complicata is clearly closely related to, and likely derived from, *G. ornata*. Smith (1938a,b) treated *G. complicata* as a full species, stating that it can always be distinguished by the absence of the saccular extension of the male valve (well-developed in *G. ornata*), in addition to the size and wing marking differences. Franclemont (1983) treated *G. complicata* as a subspecies of *G.ornata*, and both Ferguson *et al.* (2000) and Ferguson and Opler (2006) treat it as a species, but do not provide supporting data for their interpretation.

Although the saccular extension is variably developed in *ornata*, this character alone distinguishes 90% of *G. ornata* specimens from *G. complicata*. The molecular data show that some haplotypes are unique to *G. complicata* (CP1:CP3 lineage, Fig. 2-133), but additional specimens from adjacent *ornata* populations should be sequenced. Two southwest-mainland B.C. samples of *G. ornata* showed haplotypes similar to *G.complicata* haplotypes. I believe the marked difference in eye size (and probably behaviour and ecology) and wing marking characters between *G. complicata* and adjacent populations of *G. ornata* in B.C. and coastal Oregon are best interpreted as a specific differences, rather than clinal geographic variation within *ornata*.

The small size and subdued colours of *complicata* are more reminiscent of arctic-alpine species such as *G. quenseli*, with which this taxon was first associated. This moth is rarely collected, and has a very restricted global distribution. This, combined with the fact that its habitat requirements are in conflict with human development pressure, raises the possibilty of conservation concerns. This species has been treated as a subpsecies of *G. ornata*, but as noted there are considerable differences in phenotype and morphology between *G. complicata* and adjacent *G. ornata* populations (outlined above under 'Diagnosis', see also 'Remarks' under *G. ornata*).

GRAMMIA EDWARDSII (STRETCH)

FIGS. 2-39, 2-131.

Arctia edwardsii Stretch, 1872; Illust. Zygaenidae Bombycidae N. Am. 1: 77
Apantesis ornata (=edwardsi) Franclemont 1983: 117. [misspelling]
Grammia edwardsi Ferguson and Opler 2006 [misspelling]

Type Material

Described from a single male specimen from San Francisco, California [lost]. A male in good condition, but with missing right legs, labelled "Lake Merced/ S[an]. F[rancisco]. Co[unty]., Cal[ifornia].", "Collected by/ J. E. Cottle", "Barnes/ Collection", "NEOTYPE/ Arctia/ edwardsii Stretch/ B.C. Schmidt 2007" [USNM] is hereby designated as **neotype** to ensure the stability of this name. The neotype designation by Smith (1938a) was not valid since it was not published.

Diagnosis

The combination of lined forewing veins, orange hindwing, small overall size, reduced eyes, and pale buff base of the antennae are unique. May be endemic to the San Francisco Bay region of California. The wing pattern and early flight season indicate a close relationship to *G. ornata*, and the two have been treated as conspecific (e.g. Franclemont 1983). In contrast to *G. ornata*, this species has reduced eyes, narrower forewings, buff antennal scaling, is smaller overall and is likely diurnal. There is no indication of overlap in these characters in the San Francisco Bay region where the two taxa are sympatric, and there seems little doubt that the two are distinct species.

Description

The following is based on examination of one male, and the description in Smith (1938a). ***Head*** - vestiture of palps pale buff, lower half of frons pale buff, upper half and vertex dark brown; vertex pale buff laterally; eyes well developed, maximum diameter 4.93×10^{-1} mm ($n = 1$ male); male antennae moderately bipectinate, pectinations averaging 3.74×10^{-1} mm, 2.7 times longer than intersegmental distance ($n = 1$); dorsal scales of antenna black, at least basal third of antenna scaled pale buff. ***Thorax*** - Vestiture of vertex, patagia and tegulae black with broad, pale buff borders; black thorax form absent; dark brown ventrally, central tuft yellow, reduced; thorax appearing relatively smaller overall compared to *G. ornata* due to finer, less "fuzzy" scales; tibia entirely pale buff, tarsi mostly so. ***Abdomen*** - Dorsal ground colour yellowish orange, pale buff near apex; medial and lateral markings black, medial band relatively broad; pale whitish-buff ventrally, lateral black markings well developed but not confluent in males.

Forewing - Length 13.4 mm (*n* = 1 male), relatively narrow, more so than *G. ornata*; ground colour dark brown; banding pattern yellowish buff; basal and antemedial band absent; medial and postmedial well-developed, rarely extending beyond postcubital stripe; subterminal band well-developed, angled at vein M_3, not curved basad near costa; vein lines well developed; fringe entirely pale buff; costa pale and dark brown, anal margin finely pale-lined; ventrally with colours paler, and more yellowish cast; sexes similar. Hindwing - Ground colour yellow-orange; markings well developed, black, not confluent; antemedial spots discrete, streaked basad; medial spot well-developed; postmedial and subterminal spots prominent, not confluent. ***Male genitalia*** - Not examined, the following is based on Smith (1938a): distal portion of valve pointed and hooked, apex directed caudoventrally; saccular extension moderately to poorly developed, saccular process moderately developed; uncus broad-based, process evenly tapered to point; juxta 2x wider than long (Smith 1938a).

Female: female similar to male, forewing basal band well-developed; hindwing maculations discrete.

Biology

Adult dates of capture are for May through June, with a few September records possibly indicating a second generation (Smith 1938a). Nothing else is known of its biology or habitat. The reduced eye size suggests that this is likely a diurnal species.

Distribution

Known only from the San Francisco area (Lake Merced), California.

Molecular Variation

Not examined.

Remarks

The only specimens of this species originated from the San Francisco area. It has not been collected in nearly a century, and may be extinct.

GRAMMIA EUREKA FERGUSON AND SCHMIDT

FIGS. 2-25, 2-59, 2-117.

Apantesis blakei? Barnes and McDunnough, 1912: 9 pl. 3, figs. 1, 8.

Grammia eureka Ferguson and Schmidt, 2007: 42.

Type Material

Holotype male from Eureka, [Juab County], Utah, [USA]. [USNM, examined]. One male and 2 female paratypes.

Diagnosis

The males of *G. eureka* resemble those of *G. bowmani, G. nevadensis* and *G.williamsii tooele*, but have a reduced, elliptical eye and a larger, more exposed gena; the antennal branches are shorter than those of both *G. bowmani* and *G. nevadensis*, equal to those of *G. w. tooele*. The hindwing ground colour is a saturated orange-red, not pinkish as in other species. *Grammia eureka* flies in the spring, compared to late summer/early fall like most *nevadensis*-group species. Internally, the spatulate apex of the male valve is unique among *Grammia*.

Grammia eureka is sympatric with *G. n. nevadensis* and *G. williamsii tooele* in the Eureka, Utah area. The antennal and genitalic morphology, lack of pink hindwing colours and spring flight period suggest this species is more closely related to *G. ornata* than *G. nevadensis*, despite similarity of wing pattern to the latter.

Description

Head - eyes reduced (mean = 5.96×10^{-1} mm, $n = 4$), roughly equal to one-quarter of a sphere in shape, about half the size of other species in the *nevadensis* group; gena partially exposed due to reduction of eyes; dorsal margin of eye set well apart from base of antenna, nearly touching in other species; male antennae bipectinate with relatively short branches (mean 4.63×10^{-1} mm, $n = 2$), the longest 2.6 x longer than intersegmental distance; antennal scales dark brown, a few pale buff scales; female antennae slightly biserrate, scaled dark brown. ***Thorax*** - Vestiture of thorax dorsum, patagia and tegula dark brown bordered with white to pale buff; pale buff ventrally. Legs predominantly pale buff with dark brown patches. ***Abdomen*** - reddish-orange with medium-width black mid-dorsal band, pale buff ventrally with row of lateral black spots, pale-bordered at distal margin of segments; female abdomen entirely dark brown ventrally. ***Forewing*** - Nearly complete set of pale bands, but the basal and antemedial bands tending to be fragmentary, particularly in females; medial band not strongly curved basally near costa as in *G. nevadensis;* pale anal dash present; male forewing length average 16.9 mm (*n* = 2), female 18.3 (*n* = 2). Hindwing - Ground colour orange-red; dark pattern varying from only postmedial and subterminal elements to all spots present, but not suffused; ventral pattern similar, colours less intense; sexes similar. ***Male genitalia*** - Distal portion of valve distinctively squared off or spatulate distally, not rounded or tapered; juxta wide with broad, shallow dorsal notch; basal ¼ of uncus with pronounced constriction, process smoothly tapering to apex with slight constriction ⅔ of distance to apex; aedeagus with strong dorsad curve at ⅔ distance beyond base; vesica apparently indistinguishable from *G. nevadensis*, coarsely and extensively scobinate; largest, distal chamber of vesica more elongate like *G. nevadensis* in comparison to the short, nearly globose vesica of *G. williamsii*. The genitalia of only one male were examined. ***Female genitalia*** - Not examined.

Biology

Adult collection dates range from late April to mid May, suggesting this species flies in early spring, unusual among the *nevadensis* group. The reduced eyes indicate that this species is diurnal. Nothing is known of its habitat.

Distribution

Only two localities are known, at the edges of the Great Basin in central Utah and southwestern Idaho (Fig. 2-117).

Molecular Variation

Not examined, this species is known only from historical specimens.

Remarks

No specimens of *G. eureka* have turned up since the type material was collected nearly a century ago, with the exception of a female from Idaho in the 1950's. This apparent rarity is likely a result of the early flight period and probably diurnal activity.

RELATIONSHIPS WITHIN THE GENUS *GRAMMIA*

Morphology

Analysis of the morphology (MR) matrix for all *Grammia* species (Fig. 2-135) resulted in a poorly resolved phylogeny, with 100,515 most-parsimonious trees. Majority rule consensus frequencies were generally low, although the monophyly of the ingroup was well-supported (Fig. 2-135), as was the monophyly of the subgenus *Mimarctia* (Clade G; Fig. 2-135). A clade consisting of the *virguncula*-group species (*G. virguncula, G. kodara, G. quenseli,* and *G. philipiana*) was recovered as monophyletic in 75% of tree topologies (clade D, Fig. 2-135). Resolution among the remaining subgenus *Grammia* species was generally poor. About half of the species restricted to western North America were resolved as a clade in 78% of tree topolgies, the remaining western species not resolved or poorly supported as part of this clade, including *G. blakei, G. yavapai, G. elongata, G. cervinoides, G. eureka, G. fergusoni, G. complicata, G. edwardsii, G. favorita,* and *G. williamsii.*

Cytochrome oxidase I-II

The 'barcode' region of *cox1* exhibited 156 haplotypes among 227 individuals, representing 28 of the 36 species defined here. Six of the 156 haplotypes were shared among more than one species, and 17 of the 28 species sampled exhibited non-discrete haplotype clusters (Table 2-2, Fig. 2-132, 2-133, 2-134). Maximum intraspecific divergence ranged from 1.5% to 6.5% for species with five or more sampled individuals. The unusually large (>2.5%) intraspecific divergences resulted from species with paraphyletic haplotype complements (*G. elongata, G. ornata, G. parthenice, G. virguncula, G. quenseli, G. virguncula, G. williamsii;* Table 2-2); *Grammia phyllira* was the only species with a monophyletic lineage to show intraspecific variation greater than 2.5% (Table 2-2). Typical minimum *cox1-2* divergences among lepidopteran species are approximately 2% (Simon et al., 1994, Caterino et al., 2000). As discussed in Chapter 3, the high incidence of paraphyly among morphologically recognizable species is surprising, and not easily explained by typical processes resulting in non-monophyly (Funk and Omland, 2003). Thirteen species exhibited monophyletic lineages (Table 2-2), although two of these (*G. brillians, G. yukona*) showed low minimum interspecific divergences, and monophyly may be due to low sampling effort (Table 2-2).

Ten major genetic lineages were represented by all samples, partially corresponding to non-overlapping species assemblages; *G. allectans, G. incorrupta, G. ursina, G. anna, G. phyllira, G. placentia, G. virgo, G. kodara, G. arge, G. doris* all formed lineages divergent by at least 3.2% from the nearest neighbour (Fig. 2-132, Table 2-2). A significant number of species displayed haplotypes in the Western and Eastern lineages, a largely non-monophyletic assemblage of the remaining 19 species; four species (*G. elongata, G. virguncula, G. williamsii, G. quenseli*) exhibited at least one haploptype in both of these lineages, differing by at least 3.5%. These results are discussed in detail in Chapter 3.

Tree topology of the *Grammia* subset analysis using the *cox1*-barcode (BC) dataset was well-resolved, and the subgenus *Mimarctia* was again recovered as monophyletic (Fig. 2-136). Subgenus *Grammia* was paraphyletic with respect to *Mimarctia*, however, since *G. incorrupta* placed as the sister group to *Mimarctia* + *Grammia*. The combined (MR+BC) dataset did recover the two subgenera as reciprocally monophyletic (Clade F and G; Fig. 2-137), with high overall resolution. Addition of the Jerry-Pat (JP) fragment of *cox1* to the MR+BC dataset (Fig. 2-138) recovered a topology largely congruent with that of the MR+BC data, the placement of *G. incorrupta* and *G. anna* being notable exceptions, as discussed below. The congruence in topologies between the MR+BC and JP data partitions suggests that the Jerry-Pat fragment of *cox1* may be particularly informative (i.e. variable) relative to other *cox1-2* regions, and JP does indeed exhibit more nucleotide variability than BC (Chapter 3). However, regions of nucleotide diversity within *cox1-2* vary substantially among lepidopteran taxa, including among congeneric species (Roe & Sperling 2007).

Western clade (Clade A)

The Western clade (Clade A; Fig. 2-136) consisted of barcode haplotypes of the Western lineage (Fig. 2-132). The BC partition recovered this clade in most topologies (83%), although it lacked bootstrap support. There was no clear indication for monophyly of all species of this clade in the MR data, since phylogenetic resolution was low. A subset of the Western clade did show better resolution (78%), consisting of *bowmani, yukona, nevadensis, brillians* and *behrii*, but also included the *incorrupta* clade (Fig. 2-135). Although *ornata* + *hewletti* and *complicata* + *edwardsii* each formed clades, they were not sister clades as might be expected, based on the phenotypic similarity of these taxa (see species accounts).

Incorrupta clade (Clade B)

The *incorrupta* clade, consisting of *G. incorrupta, G. ursina,* and *G. allectans* haplotypes, showed high bootstrap support values in the analysis of the BC partition (Fig. 2-136). The MR dataset recovered [*incorrupta* clade + *(ornata* + *hewletti)*] as monophyletic in most topologies (82%). There was a large discrepancy in the phylogenetic position of the *incorrupta* clade among data partitions – MR data placed it as derived within subgenus *Grammia* near the *nevadensis* group (Fig. 2-135), while *cox1* data placed it as basal within the entire genus (Fig. 2-136) and the MR+BC partition resolved Incorrupta and Western as sister clades (Clade C; Fig. 2-137). This result particularly interesting given the long-standing taxonomic confusion and morphological similarly between *G. incorrupta, G. ursina,* and *G. nevadensis*, as discussed above under the species accounts. The morphological similarity of species in the the *incorrupta* and *nevadensis* groups is reflected in the MR tree topology. The placement of *G. incorrupta* as basal to [*Mimarctia* + *Grammia*] is not supported by morphology. The structural characters defining the subgenera clearly indicate *incorrupta* belongs to the subgenus *Grammia,* although potentially basal within this subgenus, as recovered in the MR+BC+JP phylogram (Fig.2-138). This would mean that much of the wing marking characters shared between the *incorrupta* and *nevadensis* groups are homoplasious, resulting from convergent evolution of wing markings. Multiple broad, pale transverse bands on the forewing (versus narrow bands and/or numerous vein lines) may be adaptive to arid habitats, since virtually identical patterns are also seen in distantly-related Palaearctic species of *Cymbalophora* (subtribe Callimorphina) and *Holarctia*, which occur in similar xeric habitats (Murzin 2003).

Eastern clade and remaining clades

There was moderate bootstrap support for the subsampled Eastern lineage haplotypes forming a clade based on the BC-only and MR+BC+JP data (Clade D; Fig. 2-136, 2-138), consisting of *G. virguncula, G. figurata, G. f-pallida* and *G. williamsii*. The MR data did not support monophyly of these species, although a clade containg *G. virguncula, G. kodara, G. quenseli, G. philipiana* was recovered in 75% of the most-parsimonious topolgies. *Grammia phyllira* and *G. placentia* were recovered as sister taxa (Clade E; Fig. 2-135, 2-137, 2-138) in all analyses with the exception of the BC data, which resolved (*placentia* + *virgo*) as sister to *phyllira*, although this relationship lacked bootstrap support. This group (*placentia, virgo, phyllira*) was recovered as monophyletic in most datasets, and may represent a basal group within the subgenus *Grammia*. Similarly, *Grammia anna* did not show close relationships to any other species or species grop in any dataset.

CONCLUSIONS

The genus *Grammia* is revised to include 36 species, six of which are described as new. Examination of morphological characters revealed that eye size, antennal structure and to a lesser extent internal genitalic structure, parallel ecological and phenotypic differences among taxa. These morphological characters therefore provide useful additional taxonomic characters. Two subgeneric groupings are well defined within *Grammia,* well-supported by morphological and molecular characters. The subgenus *Mimarctia* consists of two species, with the remaining species assigned to the subgenus *Grammia*. Within this subgenus, diagnosability of species based on genitalia alone is very low, but in conjunction with wing pattern, colour, eye and antennal structure proved very useful for delimiting species. I was unable to find genitalic characters defining species-groups within the subgenus *Grammia*, despite the fact that the molecular data largely supported groupings based on wing pattern and antennal structure.

Mitochondrial DNA did not discriminate between closely related, morphologically diagnosable species, and in some cases between distantly related species. Furthermore, several species exhibited highly divergent haplotypes, without evidence to suggest involvement of cryptic species. MtDNA revealed a deep genetic divergence between two species previously treated as conspecific, further evidence that morphology has remained remarkably consistent in the genus. Additional character systems, such as nuclear DNA, morphology of immatures, microstructure of eggs and antennae, should be sought to further resolve relationships of species groups, particularly in light of the fact that mtDNA introgression appears to be occurring among groups with apparently ancient divergences.

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Table 2-1. Taxonomic history of the genus *Grammia*

This revision	Ferguson (1985)	Franclemont (1980)	Forbes (1960)*
Grammia	*Grammia*	*Apantesis*	*Apantesis*
subgenus *Grammia*	—	—	—
subgenus *Mimarctia*	—	—	—
Holarctia turbans	(*Grammia turbans*)	(*Apantesis turbans*)	n/a*
Notarctia	*Notarctia*	(*Apantesis*)	n/a*
Apantesis	*Apantesis*	(*Apantesis*)	(*Apantesis*)

Table 2-1 (cont'd).

Munroe (1941)	Smith (1938)	McDunnough (1938)	Neumoegen & Dyar (1894)
Callarctia	*Callarctia*	*Apantesis*	*Euprepia*
subgenus *Callarctia*	subgenus *Callarctia*	—	"*Callarctia* group", in part
subgenus *Mimarctia*	subgenus *Mimarctia*	—	"*Mimarctia* group", in part
subgenus *Holarctia*	subgenus *Holarctia*	—	"*Orodemnias* group", in part
subgenus *Notarctia*	subgenus *Notarctia*	—	"*Cymbalophora* group", in part
Apantesis	*Apantesis*	(*Apantesis*)	"*Apantesis* group"

* treated only northeastern North American fauna

Table 2-2. Summary of mtDNA sample data for *Holarctia obliterata* and *Grammia* species, based on the 658 bp Barcode region of *cox1* .

Species	**Sample size**	**No. localities**	**No. haplotypes**
Holarctia obliterata	3	2	3
Grammia (Mimarctia) arge	14	4	5
Grammia (") doris	3	2	2
Grammia (Grammia) allectans	1	1	1
Grammia (") anna	6	4	6
Grammia (") behrii	3	1	3
Grammia (") blakei	2	2	1
Grammia (") bowmani	2	1	2
Grammia (") brillians	1	1	1
Grammia (") complicata	4	4	3
Grammia (") elongata	4	2	3
Grammia (") favorita	1	1	1
Grammia (") figurata	11	7	5
Grammia (") f-pallida	2	2	1
Grammia (") franconia	6	2	3
Grammia (") incorrupta	4	4	4
Grammia (") kodara	2	1	2
Grammia (") margo	4	3	2
Grammia (") nevadensis	22	16	11
Grammia (") ornata	9	9	9
Grammia (") parthenice	20	10	9
Grammia (") phyllira	8	5	7
Grammia (") placentia	6	4	4
Grammia (") quenseli	8	6	5
Grammia (") ursina	2	1	2
Grammia (") virgo	25	12	14
Grammia (") virguncula	53	25	23
Grammia (") williamsii	49	22	23
Grammia (") yukona	2	1	1
Total	**277**		**156**

Table 2-3. Comparison of characters differentiating *Grammia incorrupta* and *G. nevadensis.*

Character	***G. incorrupta***	***G. nevadensis***
Hindwing shape	Distal margin evenly rounded	Distal margin straighter
Forewing shape	Broad, distal margin relatively squared off	More pointed towards apex
Patagia	Entirely pale or striped	Entirely dark or striped
Thorax	Striped, never entirely dark	Striped or entirely dark
Male antennal branch length	> 0.70 mm, mean 0.755 mm	< 0.70 mm, mean 0.66 mm
Broods	At least double-brooded	Single brood
Female signa	large (~0.37 mm)	small (~0.24 mm)
Light attraction	Males and females	Males only

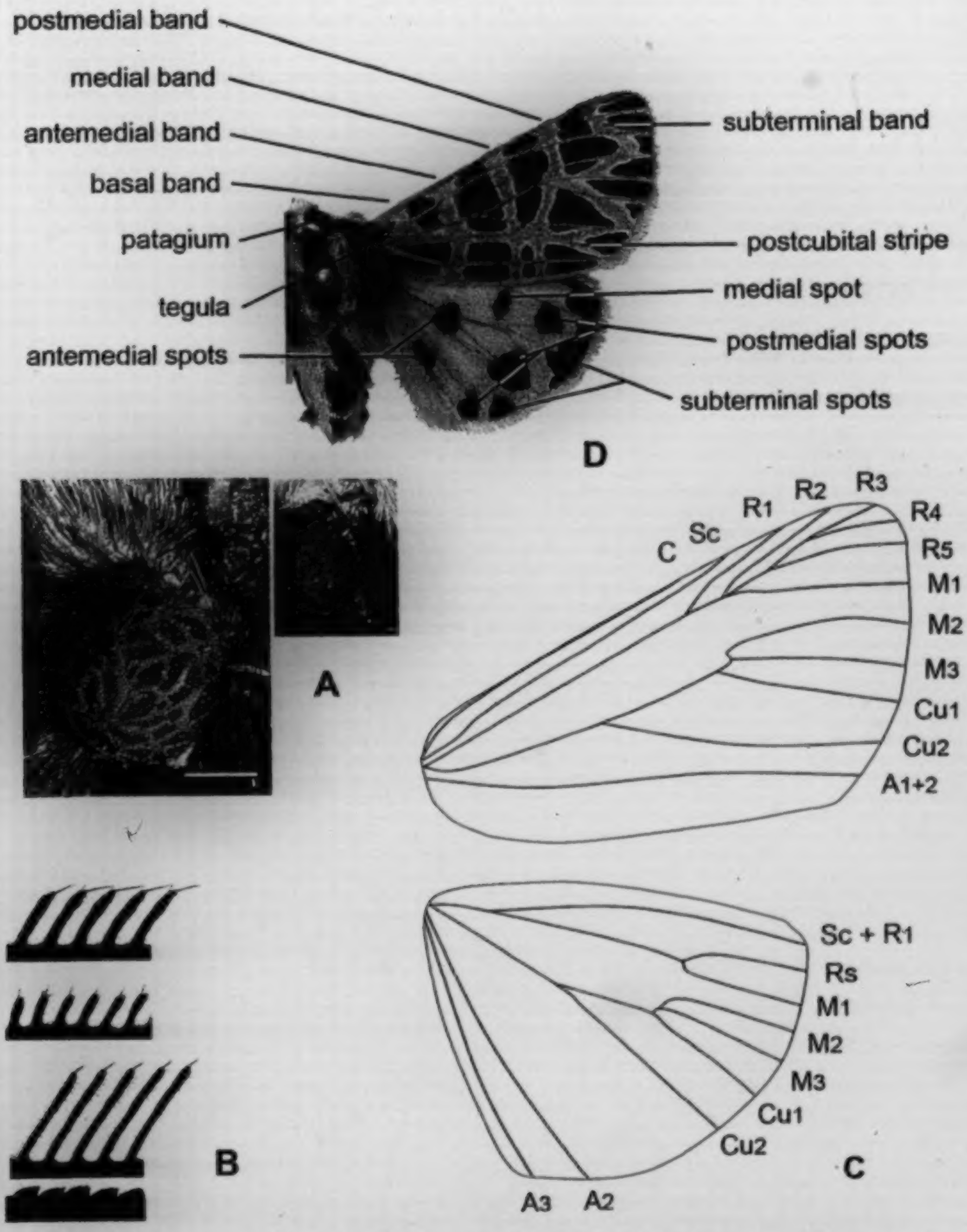
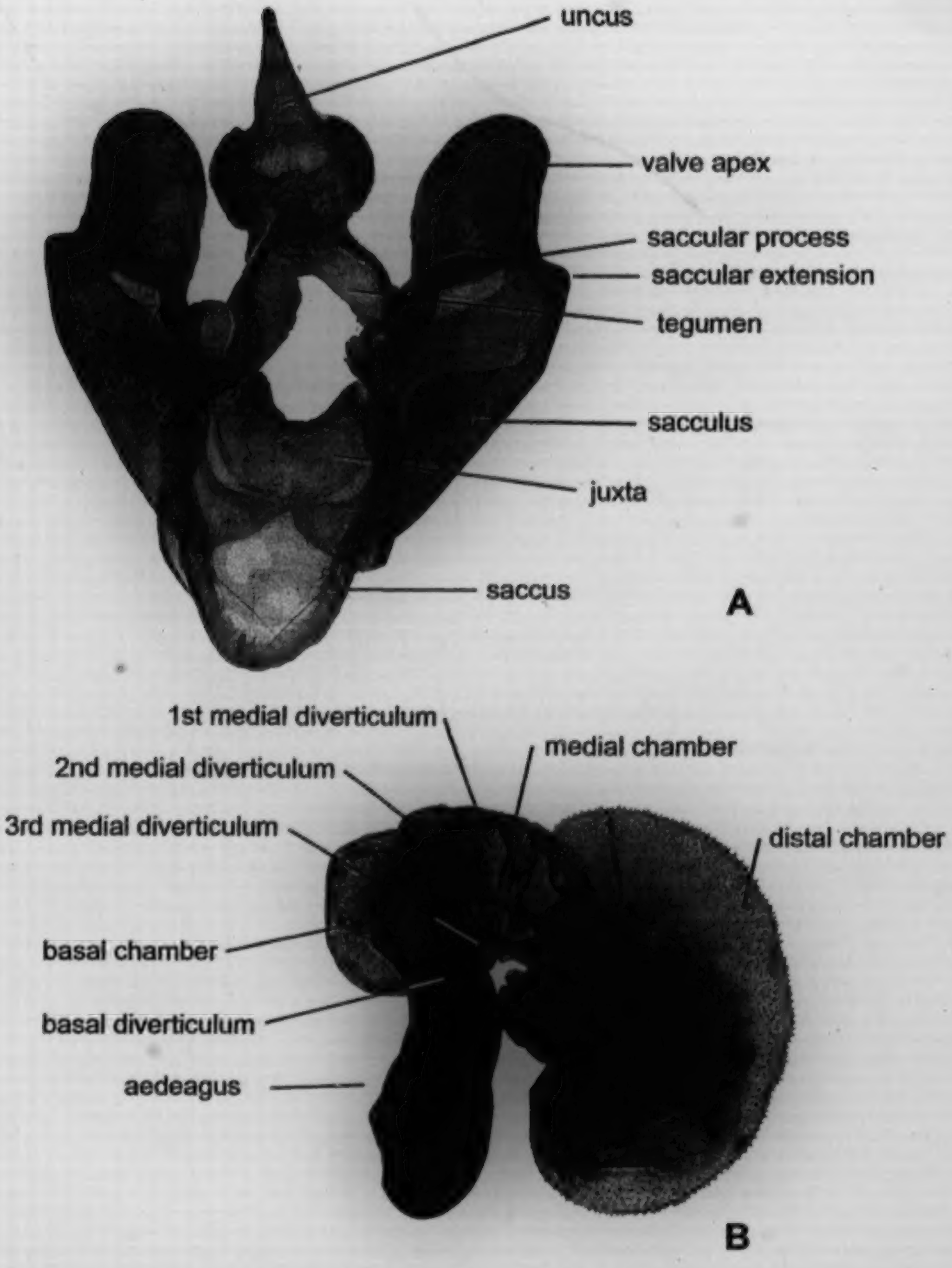

postmedial band
medial band
antemedial band
basal band
patagium
tegula
antemedial spots
subterminal band
postcubital stripe
medial spot
postmedial spots
subterminal spots
D
A
C
Sc
R1
R2
R3
R4
R5
M1
M2
M3
Cu1
Cu2
A1+2
Sc + R1
Rs
M1
M2
M3
Cu1
Cu2
A3
A2
B
C

Figure 2-1. External morphological features of *Grammia*. **1a**. Typical eye of nocturnal *Grammia* (left, *G. incorrupta*) and reduced, ellipsoid eye of diurnal species (right, *G. quenseli*). **1b**. Posterior antennal pectinations showing variation in branch length from (top to bottom) moderate to reduced and well-developed in males, and serrate (females). **1c**. Generalized wing venation of *Grammia*. **1d**. Wing pattern terminology used herein, following Ferguson (1985).


uncus
valve apex
saccular process
saccular extension
tegumen
sacculus
juxta
saccus
A
1st medial diverticulum
medial chamber
2nd medial diverticulum
3rd medial diverticulum
distal chamber
basal chamber
basal diverticulum
aedeagus
B

Figures 2-2a, 2-2b. Terminology of genitalic structures in male *Grammia*, for: **2a**. male genitalic capsule (ventral view), and **2b.** male aedeagus and vesica (right lateral view).

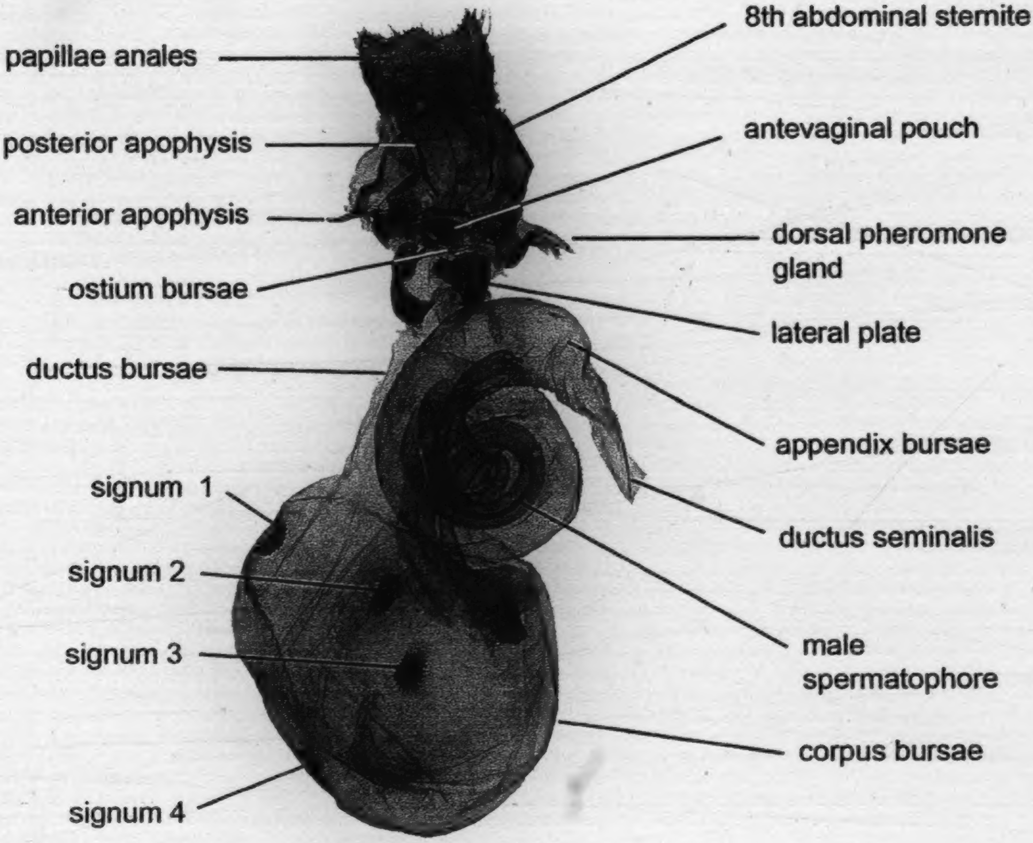

papillae anales
8th abdominal sternite
posterior apophysis
antevaginal pouch
anterior apophysis
dorsal pheromone gland
ostium bursae
lateral plate
ductus bursae
appendix bursae
signum 1
ductus seminalis
signum 2
signum 3
male spermatophore
corpus bursae
signum 4

Figure 2-2c. Terminology of genitalic structures in female *Grammia* (right ventro-lateral view, 8th sternite vomitted).

Plate I. Habitus of adult *Holarctia obliterata* and *Grammia.*
(scale bar = 1 cm)

2-3) *H. obliterata* (Stretch) - A) ♂. AB: Kootenay Plains Ecol. Res., Whirlpool Pt. **B)** ♀. AB: Nordegg.

2-4) *G. arge* (Drury) - A) ♂. ON: Carp Ridge. **B)** ♀. ON: Pakenham alvar.

2-5) *G. doris* (Bdv.) - A) ssp. *doris* (Bdv.) ♂. SC: Berkeley Co., McClellanville, Wedge. **B)** ssp. *doris* (Bdv.) ♀. SC: Berkeley Co., McClellanville. **C)** ssp. *minea* (Bdv.) ♂. AB: Peace River, Twp. 84 Rge. 22 W5.

2-6) *G. phyllira* (Drury) - A) ♂. ON: Stittsville, Jinkinson Rd. **B)** ♂. AB: Siegner Lake sandhills. **C)** ♀. AB: Wainwright Dunes Ecol. Res.

2-7) *G. placentia* (J. E. Smith) - A) ♂. FL: Alachua Co., Gainesville. **B)** ♀. FL: Putnam Co., Welaka Forest.

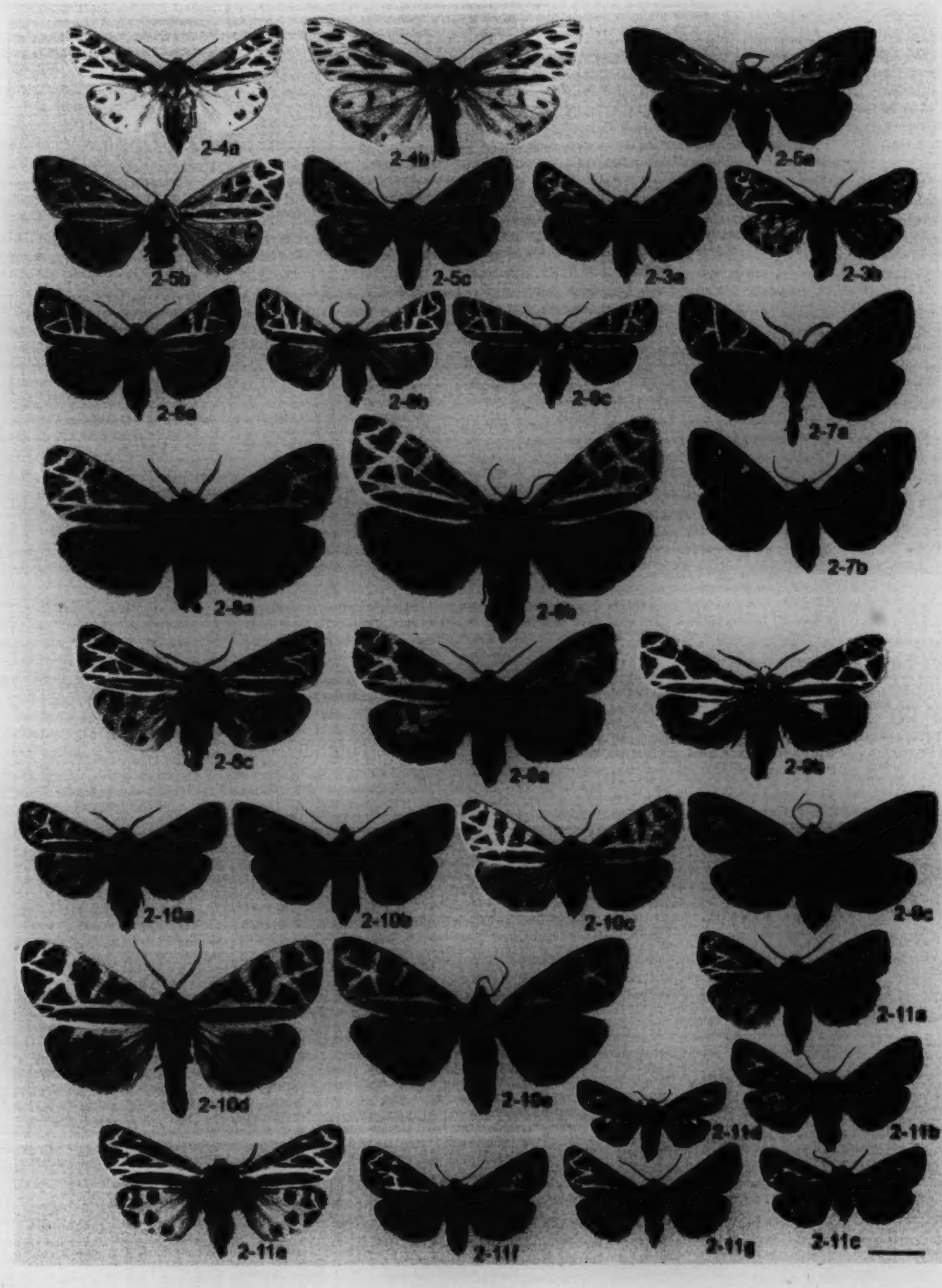
2-8) *G. virgo* (L.) – A) ssp. *virgo* (L.) ♂. ON: Stittsville. **B)** ssp. *gigas* Schmidt ♀. Holotype. NC: Highlands. **C)** ssp. *virgo* (L.). AB: Tolman Bridge.

2-9) *G. anna* (Grt.) - A) ♂. ON: Carp Ridge. **B)** ♂. ON: Carp Ridge. **C)** ♀. [no data].

2-10) *G. parthenice* (W. Kby.) – A) ♂. Neotype. AB: Chauvin, 13km N. **B)** ON: Carp Ridge. **C)** ♂. MT: Belt, 2 mi. SE. **D)** ♂. GA: Houston Co., Big Grocery Ck. **E)** ♀. GA: Whitfield Co., Rocky Face.

2-11) *G. virguncula* (W. Kby.) – A) ssp. *virguncula* ♂. Neotype. ON: Carp Ridge. **B)** ssp. *virguncula* (W. Kby.) ♀. AB: Edmonton. **C)** ssp. *speciosa* (W. Kby.) ♂. QC: Mistassini. **D)** ssp. *speciosa* (W. Kby.) ♀. AB: Birch Mtns. Wildland Park, Sand River. **E)** ssp. nr. *virguncula* (W. Kby.) ♂. NE: Omaha. **F)** ssp. *celineata* Schmidt ♀. Paratype. AB: Nordegg. **G)** ssp. *celineata* Schmidt ♂. Holotype. AB: Bragg Creek, 25 km SW.

Plate I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2-10e
2-11a
2-11d
2-11b
2-11e
2-11f
2-11g
2-11c

Plate II. Habitus of adult *Grammia*.

(scale bar = 1 cm)

2-12) *G. kodara* Dubatolov & Schmidt - A) ♂. Paratype. Russian Federation, Kodar Mtns., Kodar village. **B)** ♀. Paratype. Russian Federation, Kodar Mtns., Kodar village.

2-13) *G. philipiana* Ferguson - A) ♂. Holotype. AK: McKinley N.P., Reflection Pond. **B)** ♀. Allotype. AK: Ray Mtns., nr. Torment Ck.

2-14) *G. quenseli* (Paykull) - A) ♂. YT: British Mtns. **B)** ♀. YT: 40 km W Dawson. **C)** ♂. MB: 24 km NE Churchill. **D)** ♀. MB: 24 km NE Churchill.

2-15) *G. margo* Schmidt – A) ♂. Holotype. AB: 7.5km SE Edgerton. **B)** ♀. Paratype. AB: Red Deer.

2-16) *G. franconia* (H. Edw.) – A) ♂. ON: Carp Ridge. **B)** ♀. ON: Carp Ridge.

2-17) *G. figurata* (Drury) – A) ♂.KS: Trego Co., Cedar Bluff St. Pk. **B)** ♂. ON: St. Williams. **C)** ♂. ON: St. Williams. **D)** ♀. NJ: Lakehurst.

2-18) *G. f-pallida* (Stkr.) - A) ♂. CO: Baca Co., Comanche Nat Grassland. **B)** ♂. CO: Clear Creek Co., Mt. Evans, 10,600'.

2-19) *G. incorrupta* (Hy. Edwards) - A) ♂. CO: Baca Co., Comanche Nat Grassland. **B)** ♂. AZ: Yavapai Co., Granite Dells, 4 mi N. **C)** ♀. AZ: Santa Cruz Co., Santa Rita Mtns, nr. Sonoita.

2-20) *G. allectans* Ferguson ♂. Durango: 10 mi W El Salto 9000'.

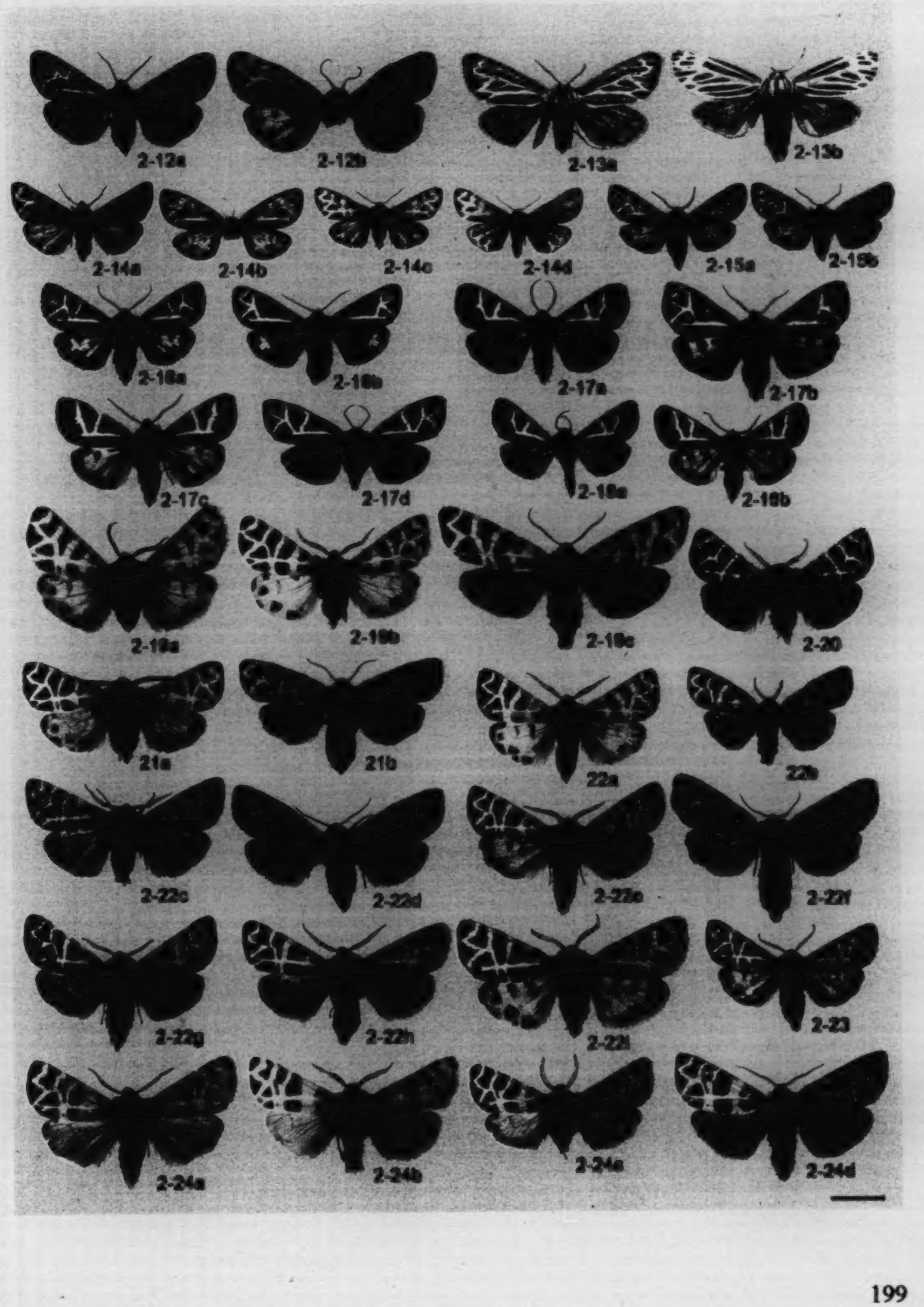
2-21) *G. ursina* Schmidt – A) ♂. Paratype. CA: San Diego Co., MCAS Miramar. **B)** ♀. Paratype. CA: Riverside Co., Lake Matthews.

2-22) *G. nevadensis* (G. & R.) – A) ssp. *nevadensis* ♂. NV: Humboldt Co., 17km N Winnemuca. **B)** ssp. *nevadensis* ♀. CA: Inyo Mtns. **C)** ssp. *superba* (Stretch) ♂. BC: Royal Oak, Saanich. **D)** ssp. *superba* (Stretch) ♀. BC: Victoria, Mt. Douglas, Saanich. **E)** *G. n. nevadensis / superba* intergrade ♂. WA: Umptanum Ck. **F)** *G. n. nevadensis / superba* intergrade ♀. BC: Kanaka Bar. **G)** ssp. *vivida* Schmidt ♂. Holotype. AB: Kootenay Plains Ecol. Res., Whirlpool Pt. **H)** ssp. *gibsoni* (McD.) ♂. SK: Burstall. **I)** ssp. *geneura* (Stkr.) ♂: CO: Larimer Co., Estes Park 7800'.

2-23) *G. yukona* Schmidt ♂. Holotype. YT: Kusawa Lake.

2-24) *G. behrii* (Stretch) - A) ♂. OR: Josephine Co, Eight Dollar Mtn Rd 1125'. **B)** ♂. CA: Los Angeles Co., Mojave Desert, Juniper Hills 3500'. **C)** ♂. CA: Kern Co., Greenhorn Mtns., Oak Flat lookout 4600'. **D)** ♀. CA: Los Angeles Co., Sierra Pelona Vly., mi 3 Anthony Rd. off Mint Cyn. Hwy.

Plate II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2-22i
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2-24a
2-24b
2-24c
2-24d

Plate III. Habitus of adult *Grammia.*
(scale bar = 1 cm)

2-25) *G. eureka* Ferguson & Schmidt – A) ♂. Holotype. UT: Juab Co., Eureka. **B)** ♀. Paratype. ID: Boise, Ada Co.

2-26) *G. bowmani* Ferguson & Schmidt ♂. Paratype. CO: Mesa Co., Black Ridge, Coal Mine Pt. 7000'.

2-27) *G. brillians* Schmidt ♂. Holotype. UT: Garfield Co., Bryce Cyn. NP, Water Cyn. 6800'.

2-28) *G. williamsii* (Dodge) - A) ssp. *williamsii* ♂. AB: Jasper NP, Pyramid L. **B)** ssp. *williamsii* ♂. AB: Jenner, 10km N. **C)** ssp. *williamsii* ♂. AB: Sandy Point, Hwy 41 at S. Saskatchewan R. **D)** ssp. *williamsii* ♀. AB: Grande Prairie, Kleskun Hill. **E)** ssp. *tooele* (B. & McD.) ♂. UT: Nephi, 7 mi NE 6700'.

2-29) *G. favorita* (Neum.) ♂. CO: Weld Co., Roggen.

2-30) *G. yavapai* Schmidt – A) ♂. Holotype. AZ: Coconino Co., Parks 7100'. **B)** ♀. Paratype. AZ: Coconino Co., Williams.

2-31) G. *bolanderi* (Stretch) ♂. Holotype. CA: Mt. Shasta [reproduction of original illustration].

2-32) *G. blakei* (Grt.) – A) ♂. AB: Tolman Bridge, Red Deer R. E Trochu. **B)** ♀. AB: Hilda.

2-33) *G. cervinoides* (Stkr.) – A) ♂. CO: Park Co. **B)** ♀. CO: Park Co., Horseshoe Gulch, Peerless Mtn Rd 12,000'.

2-34) *G. elongata* (Stretch) – A) ♂. AB: Bragg Creek, 22km W, Jumpingpound Ridge. **B)** ♀. AB: Waterton Lakes.

2-35) *G. fergusoni* Schmidt - A) ♂. Paratype. CA: Tuolumne Co., Sonora Pass 9623'. **B)** ♀. Paratype. CA: Mono Co., Lake Marie.

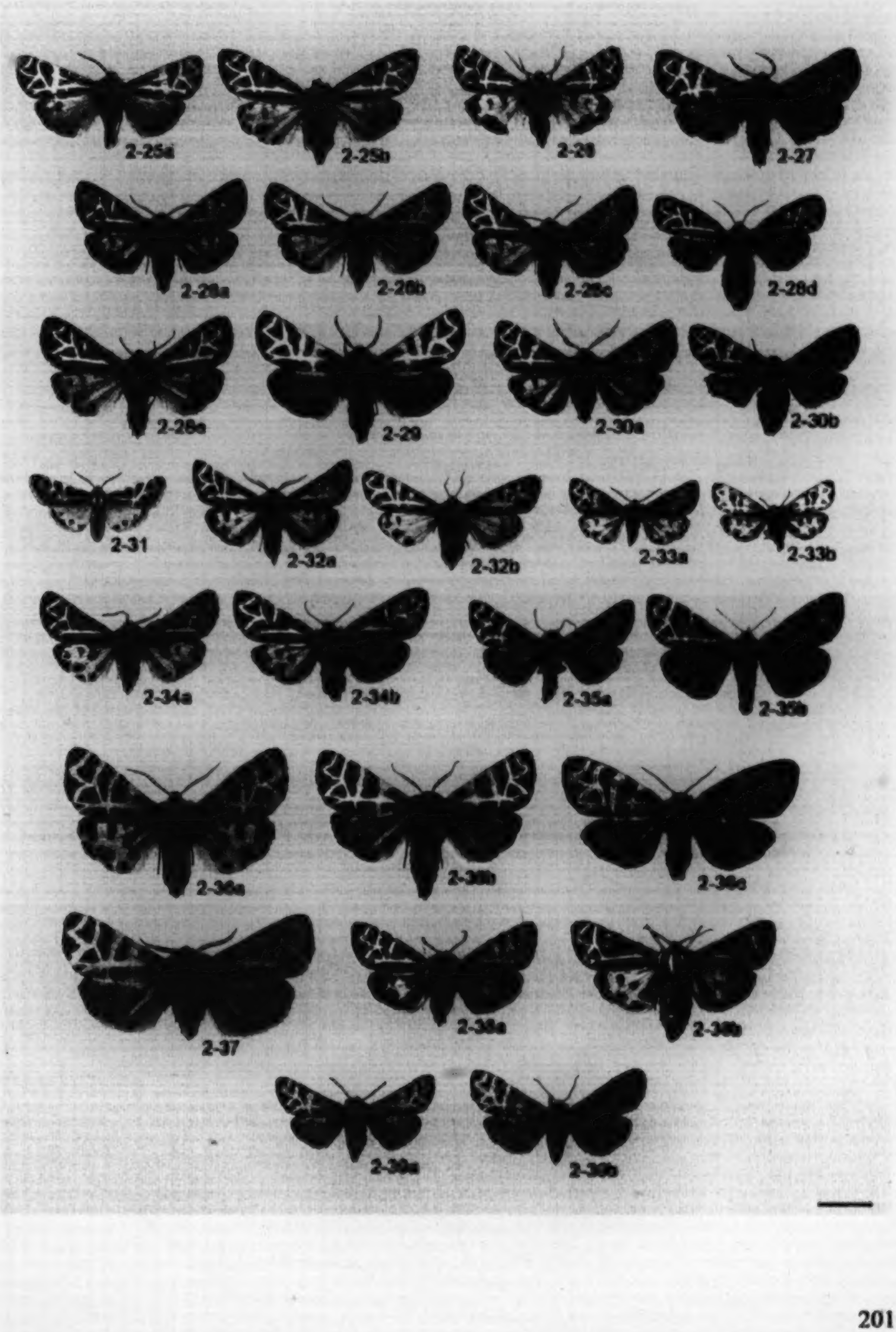
2-36) *G. ornata* (Pack.) – A) ♂. CA: Plumas Co., Squirrel Ck. 5800'. **B)** ♂. BC: Kikomun Ck. **C)** ♀. BC: Summerland, Garnet Valley.

2-37) *G. hewletti* (B. & McD.) ♂. CA: San Diego Co., 3mi E Julian.

2-38) *G. complicata* (Walker) – A) ♂. BC: Wellington. **B)** ♀. BC: Victoria .

2-39) *G. edwardsii* (Stretch) – A) ♂. CA: San Francisco Co., Lake Merced. **B)** ♀. [no data].

Plate III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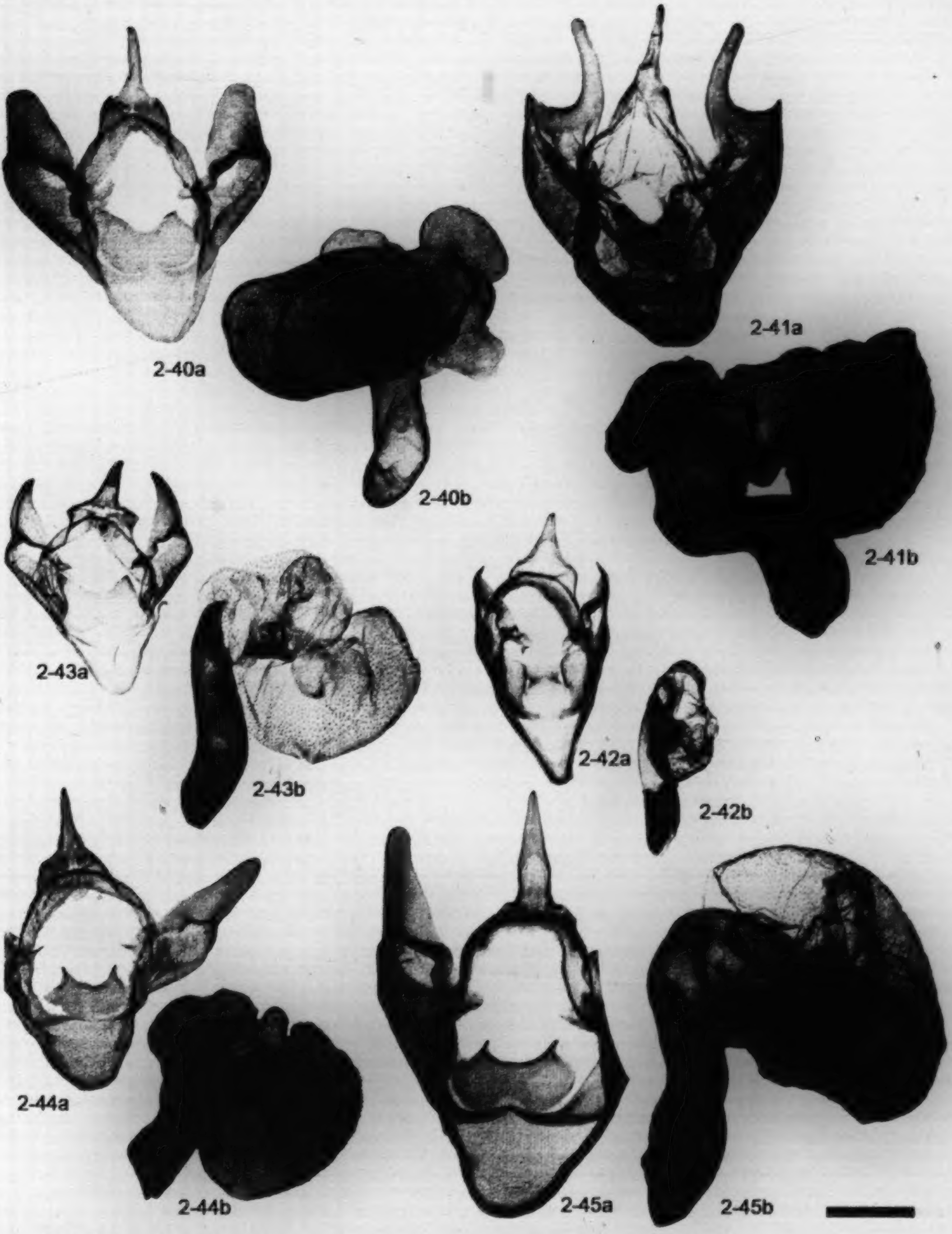
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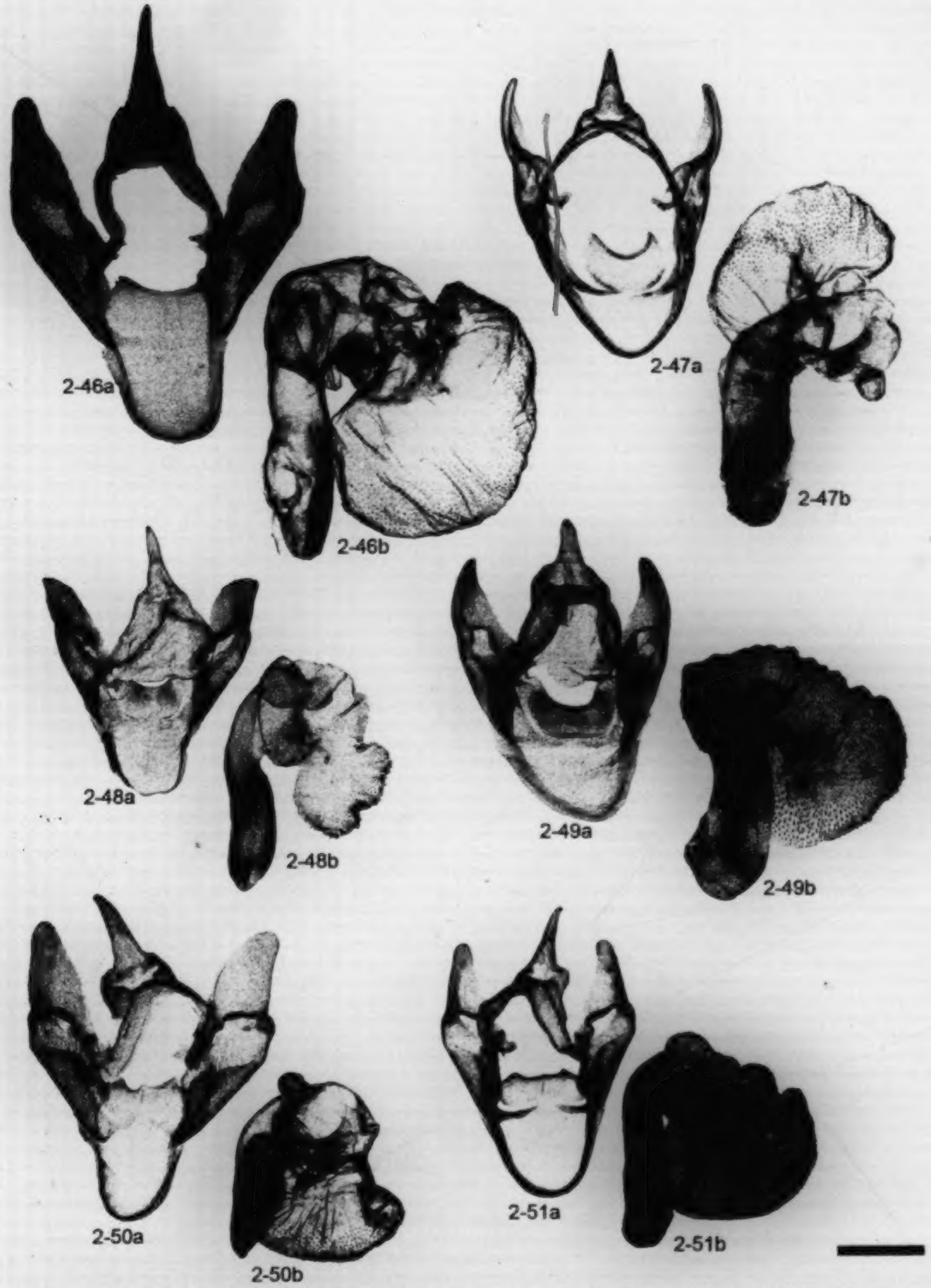
2-45a
2-45b

Figs. 2-40 – 2-45. Genitalia of male *Holarctia* and *Grammia*, ventral aspect of valve and right lateral aspect of aedeagus. 2-**40.** *G. arge* (Drury). 2-**41.** *G. doris doris* (Bdv.). 2-**42.** *Holarctia obliterata* (Stretch). 2-**43.** *G. phyllira* (Drury). 2-**44.** *G. placentia* (J. E. Smith). **2-45.** *G. virgo virgo* (L.). Scale bar equals 1 mm.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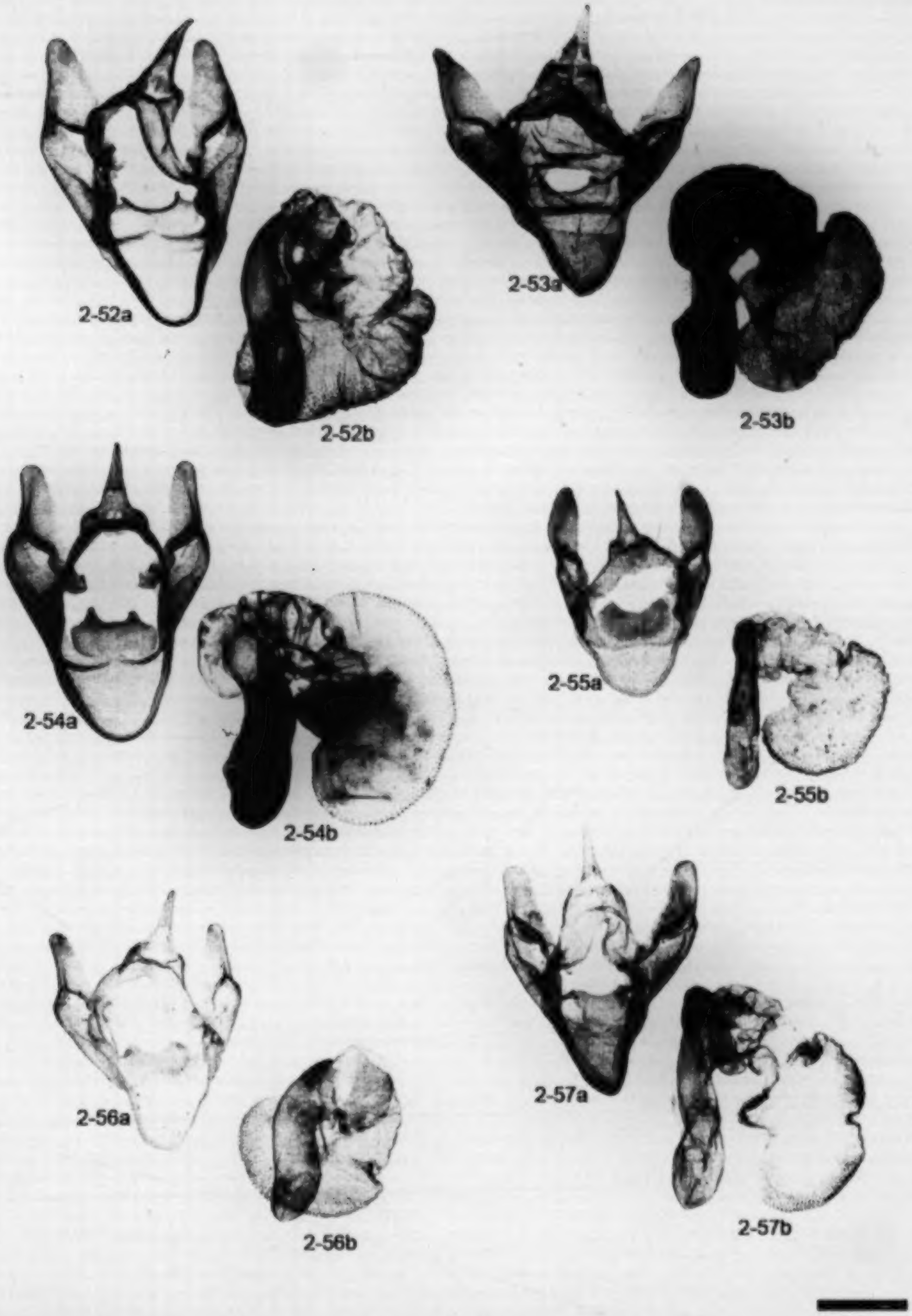
2-51b

Figures 2-46 – 2-51. Genitalia of male *Grammia*. **2-46.** *G. anna* (Grt.). **2-47.** *G. parthenice* (W. Kby.). **2-48.** *G. quenseli* (Paykull). **2-49.** *G. virguncula* (W. Kby.). **2-50.** *G. margo* Schmidt.**2-51.** *G. franconia* (H. Edw.).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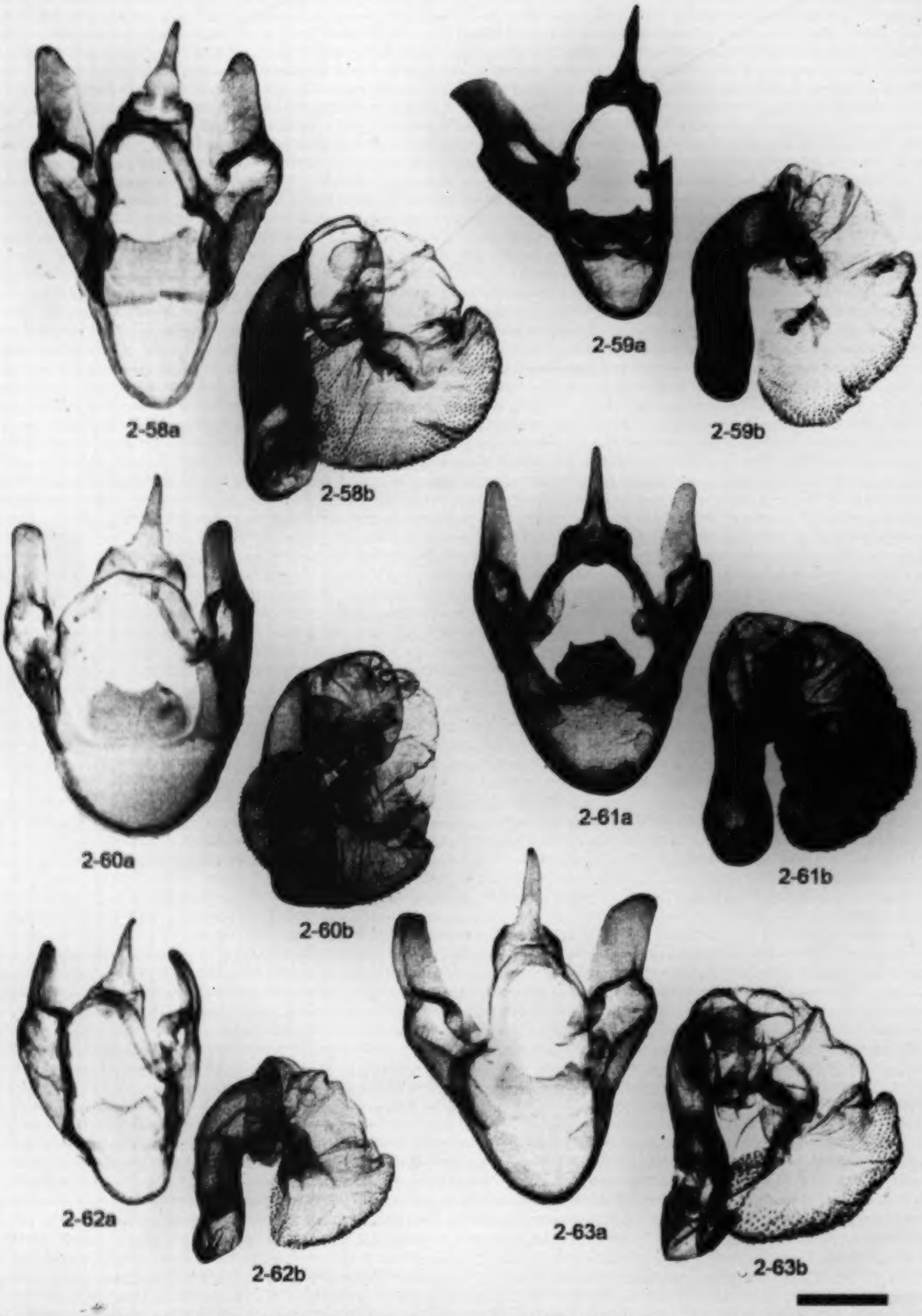
Figures 2-52 to 2-57. Genitalia of male *Grammia*. **2-52.** *G. figurata* (Drury). **2-53.** *G. f-pallida* (Stkr.). **2-54.** *G. incorrupta* (Hy. Edwards). **2-55.** *G. allectans* Ferguson. **2-56.** *G. ursina* Schmidt. **2-57.** *G. nevadensis* (G. & R.).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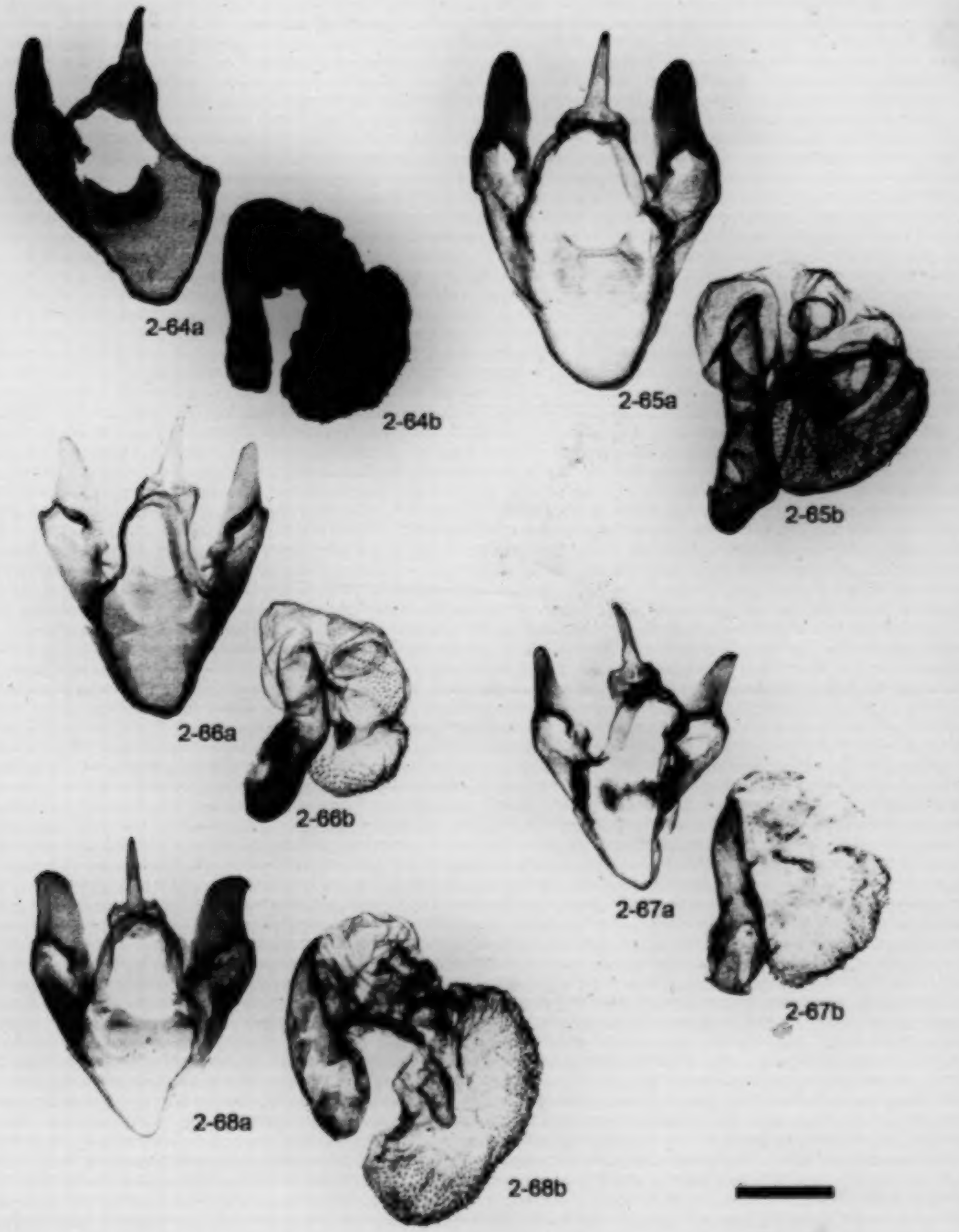
Figures 2-58 – 2-63. Genitalia of male *Grammia*. **2-58.** *G. behrii* (Stretch). **2-59.** *G. eureka* Ferguson & Schmidt. **2-60.** *G. brillians* Schmidt. **2-61.** *G. bowmani* Ferguson & Schmidt. **2-62.** *G. williamsii* (Dodge). **2-63.** *G. elongata* (Stretch).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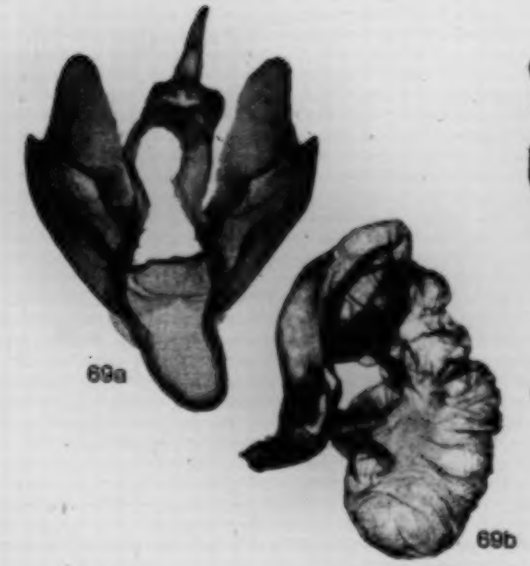
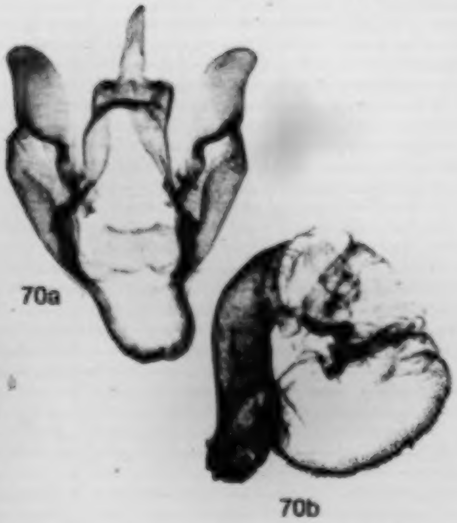
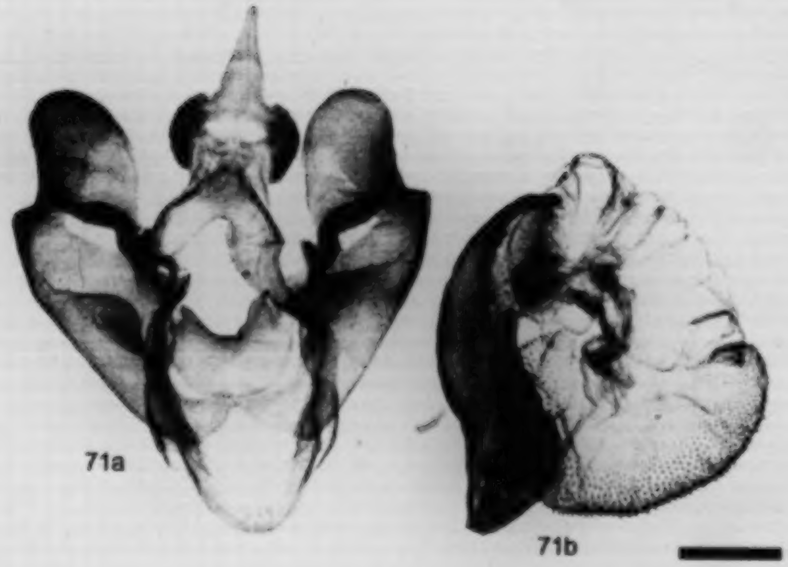
2-67b
2-68a
2-68b

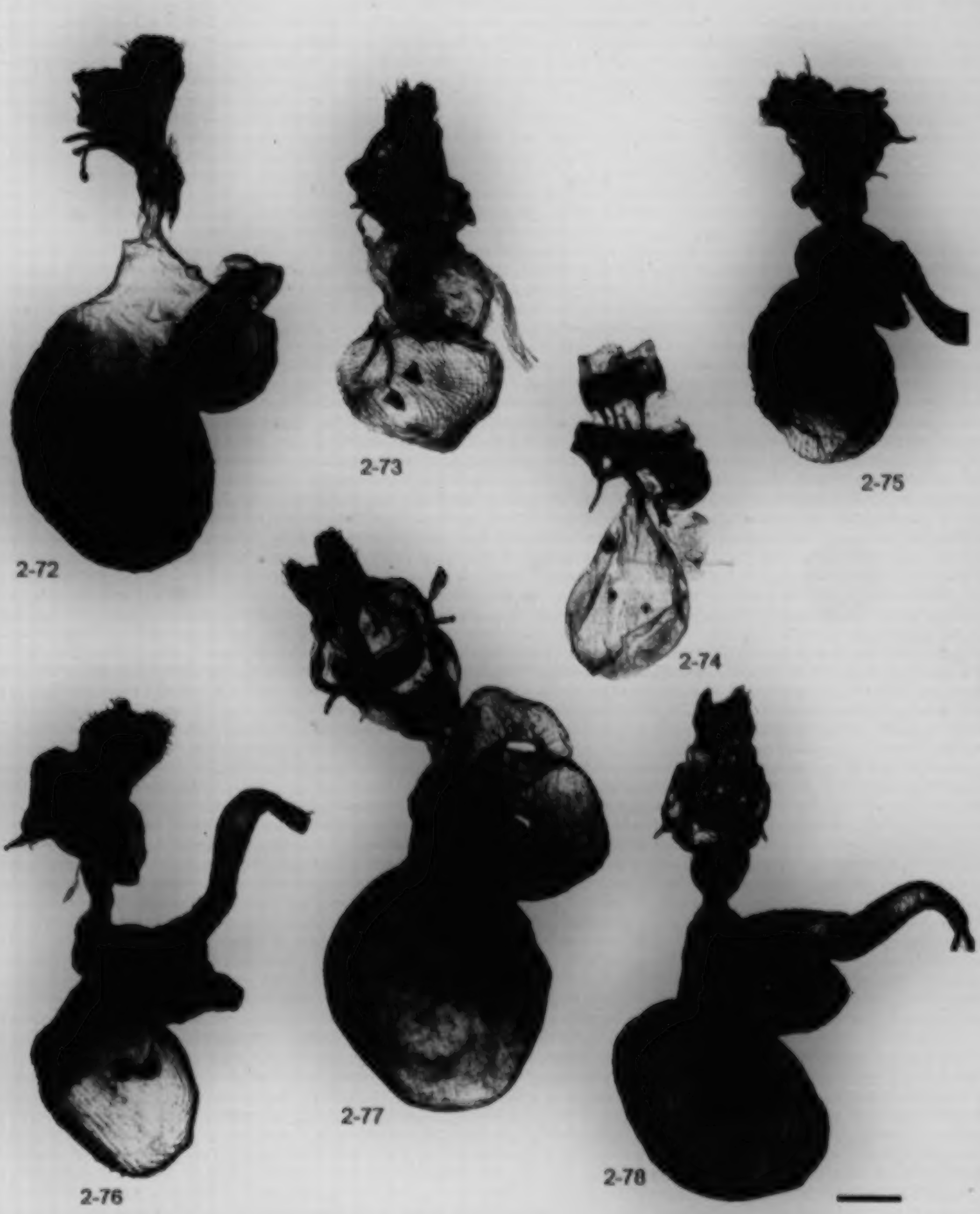
Figures 2-64 – 2-68. Genitalia of male *Grammia*. **2-64.** *G. yavapai* Schmidt. **2-65.** *G. favorita* (Neum.). **2-66.** *G. blakei* (Grt.) **2-67.** *G. cervinoides* (Stkr.). **2-68.** *G. fergusoni* Schmidt.







Figs. 2-69 – 2-71. Genitalia of male *Grammia*. **2-69.** *G. ornata* (Pack.). **2-70.** *G. complicata* (Walker). **2-71.** *G. hewletti* (B. & McD.).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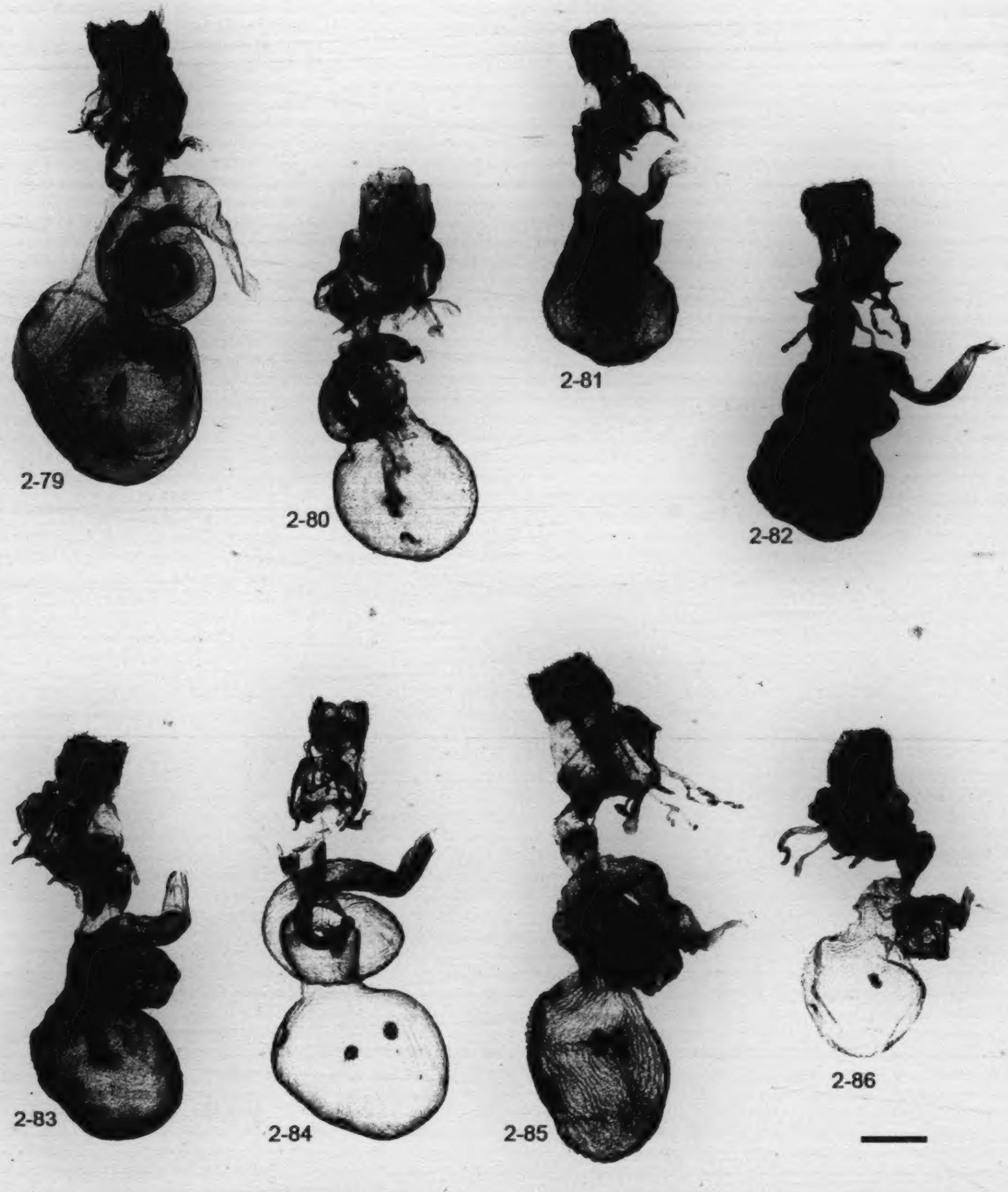
Figures 2-72 – 2-78. Genitalia of female *Holarctia* and *Grammia*, ventral aspect. **2-72.** *G. arge* (Drury). **2-73.** *G. doris* (Bdv.). **2-74.** *H. obliterata* (Stretch). **2-76.** *G. phyllira* (Drury). **2-76.** *G. placentia* (J. E. Smith). **2-77.** *G. virgo* (L.). **2-78.** *G. parthenice* (Kby.).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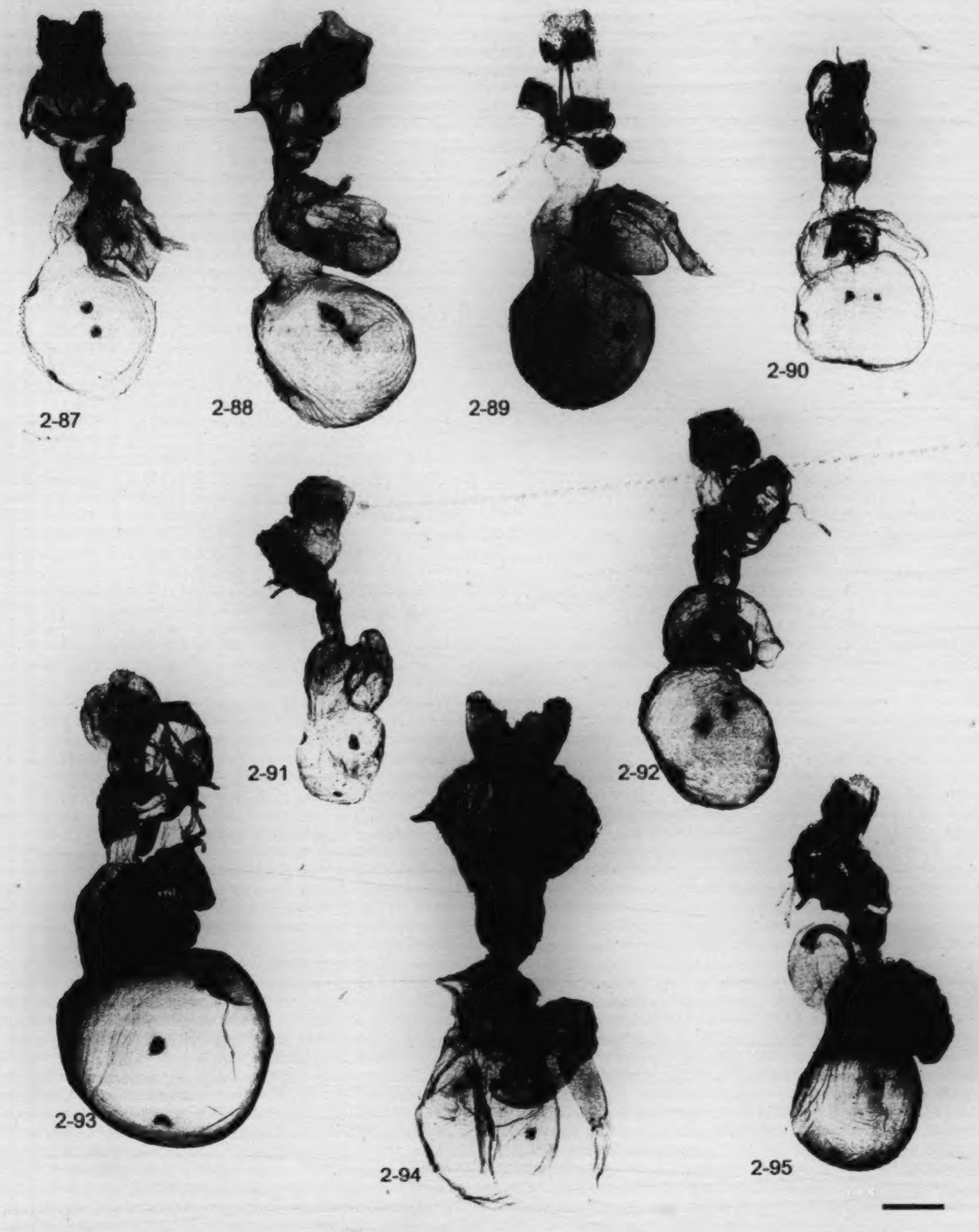
Figures. 2-79 – 2-86. Genitalia of female *Grammia*, ventral aspect. **2-79.** *G. virguncula* (W. Kby.). **2-80.** *G. quenseli* (Paykull). **2-81.** *G. margo* Schmidt. **2-82.** *G. franconia* (H. Edw.). **2-83.** *G. figurata* (Drury). **2-84.** *G. f-pallida* (Stkr.). **2-85.** *G. incorrupta* (Hy. Edwards). **2-86.** *G. ursina* Schmidt.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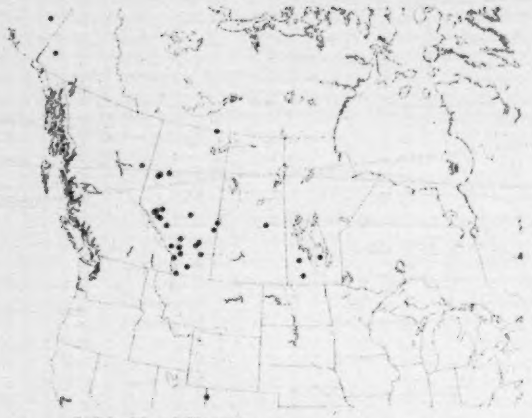
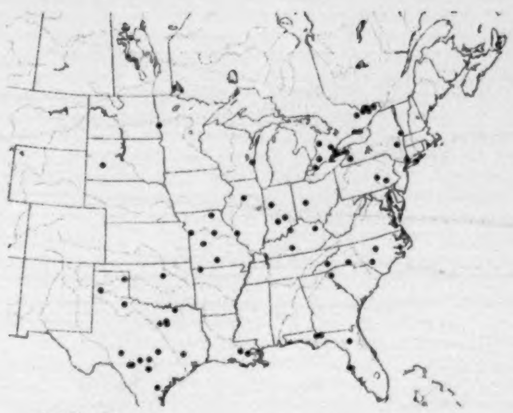
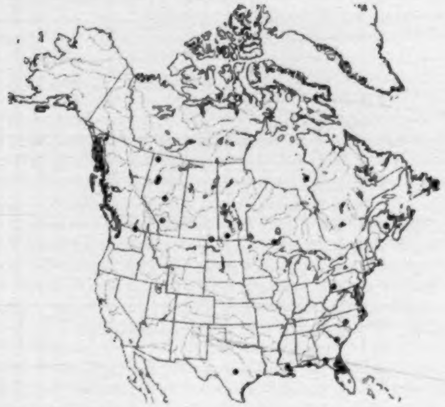
Figures 2-87 – 2-95. Genitalia of female *Grammia*, ventral aspect. **2-87.** *G. nevadensis* (G. & R.). **2-88.** *G. behrii* (Stretch). **2-89.** *G. williamsii* (Dodge). **2-90.** *G. elongata* (Stretch). **2-91.** *G. blakei* (Grt.). **2-92.** *G. fergusoni* Schmidt. **2-93.** *G. ornata* (Pack.). **2-94.** *G. hewletti* (B. & McD.). **2-95.** *G. complicata* (Walker).



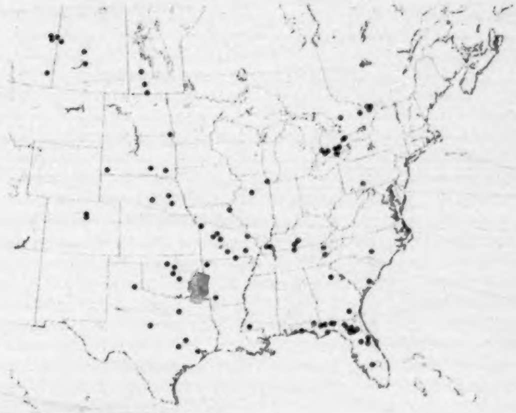
2-96. *H. obliterata.*



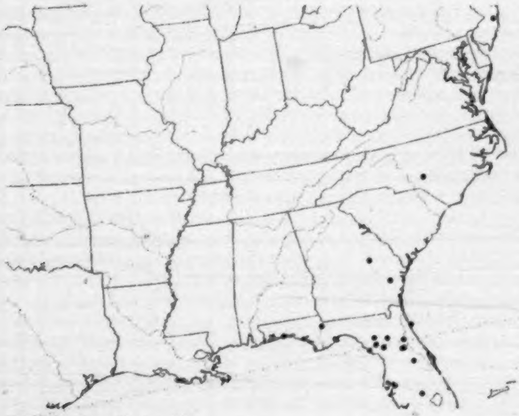
2-97. *G. arge.*



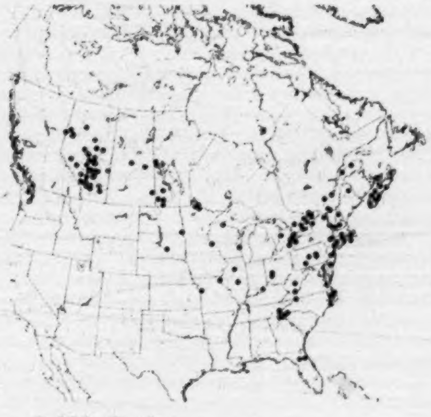
2-98. *G. doris.*



2-99. *G. phyllira.*

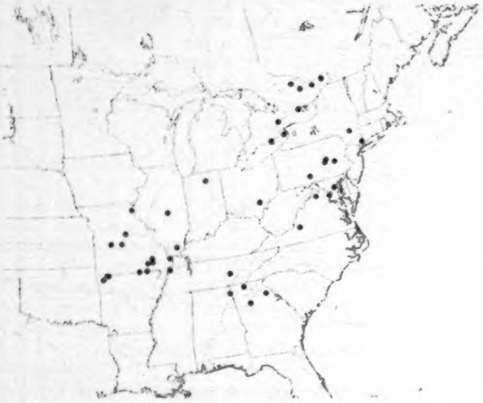


2-100. *G. placentia.*

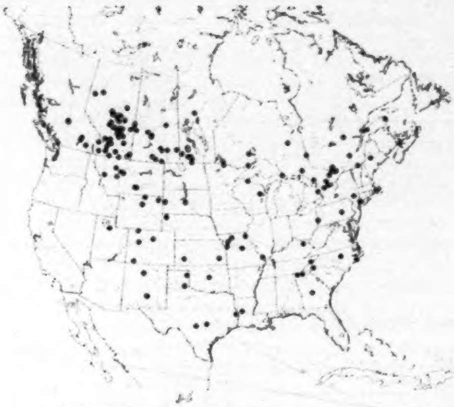


2-101. *G. virgo.*

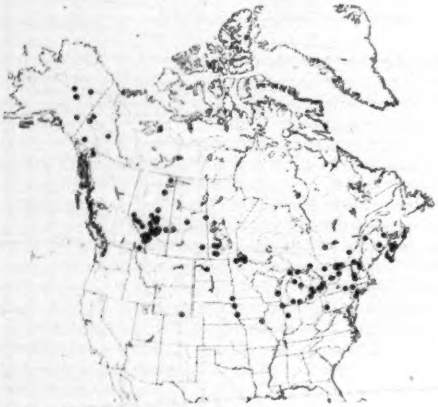
Figures 2-96 - 2-101. Distribution of examined specimens of *Holarctia* and *Grammia.*



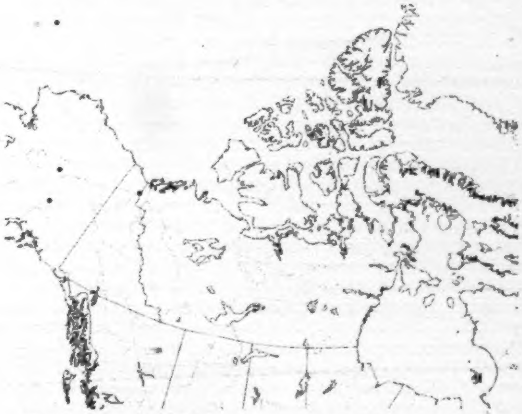
2-102. *G. anna.*



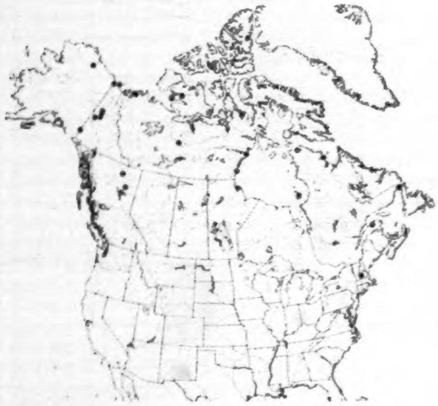
2-103. *G. parthenice.*



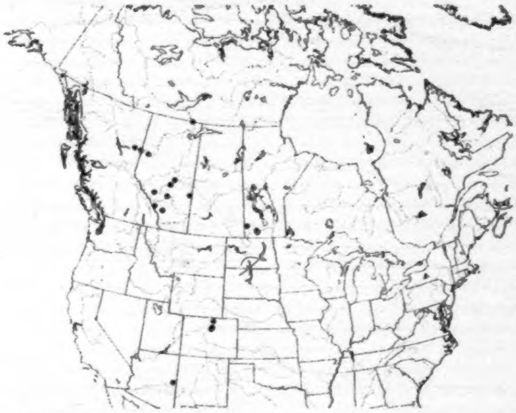
2-104. *G. virguncula.*



2-105. *G. philipiana.*

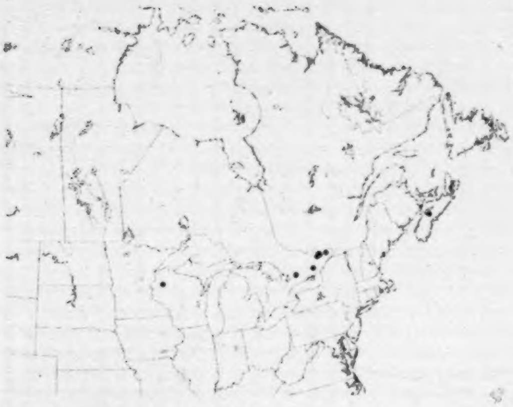


2-106. *G. quenseli.*

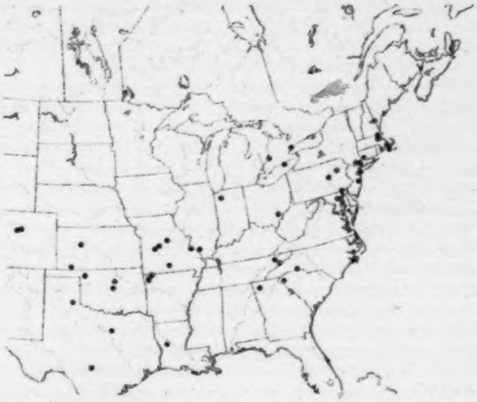


2-107. *G. margo.*

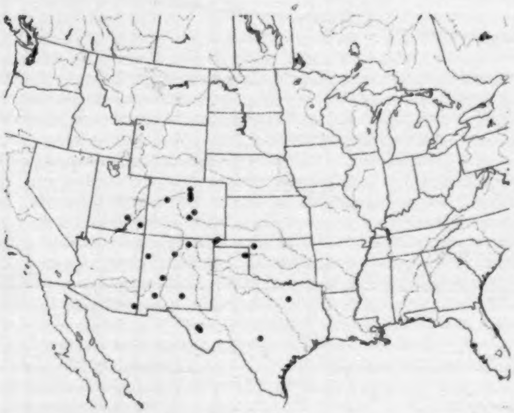
Figures 2-102 - 2-107. Distribution of examined specimens of *Grammia*.



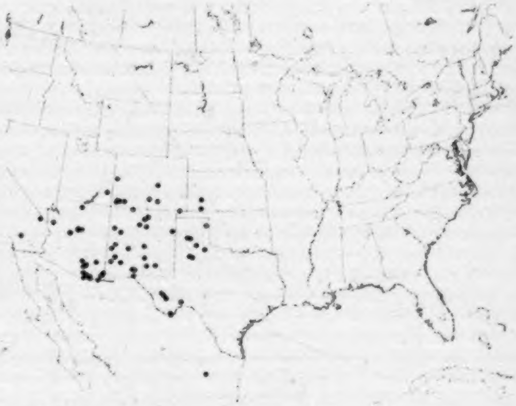
2-108. *G. franconia*



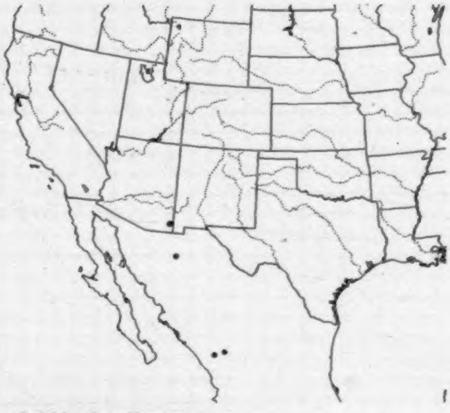
2-109. *G. figurata.*



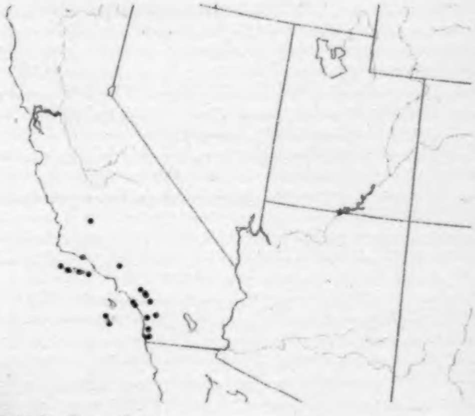
2-110. *G. f-pallida.*



2-111. *G. incorrupta.*

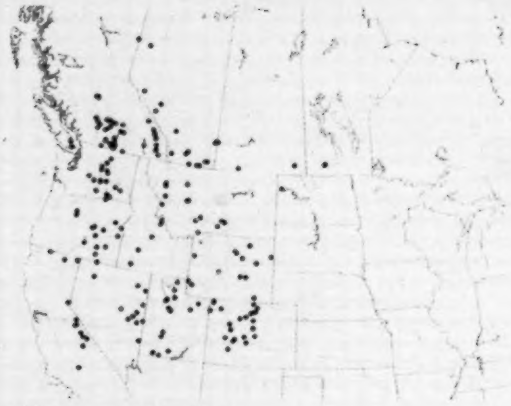


2-112. *G. allectans.*

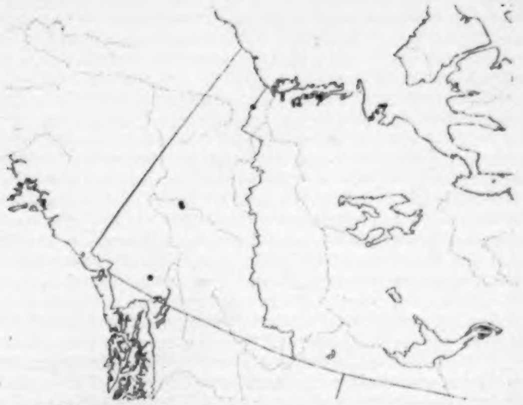


2-113. *G. ursina.*

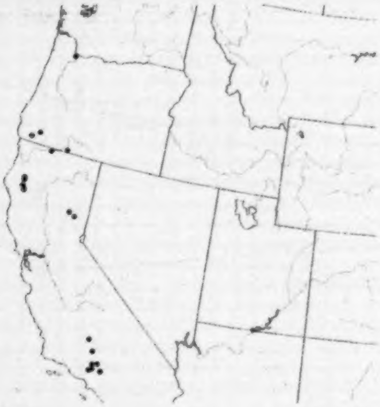
Figures 2-108 - 2-113. Distribution of examined specimens of *Grammia*.



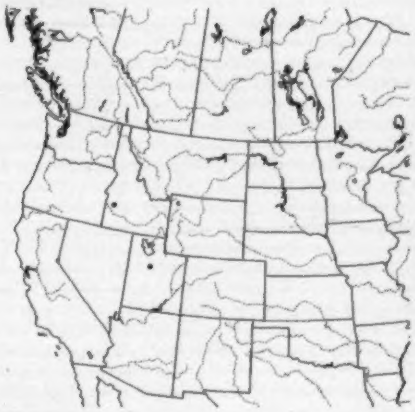
2-114. *G. nevadensis.*



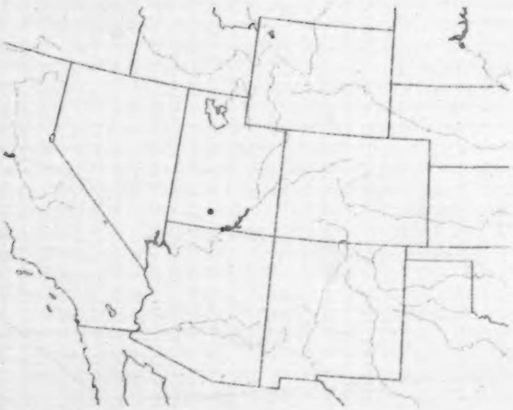
2-115. *G. yukona.*



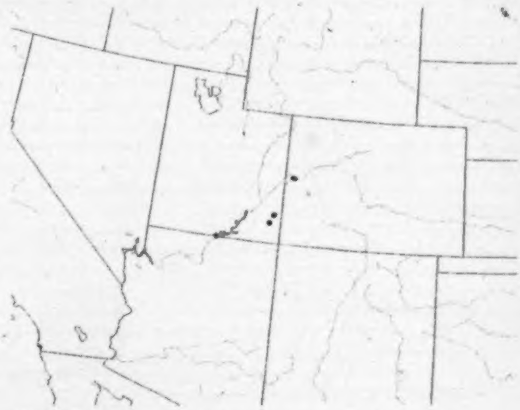
2-116. *G. behrii.*



2-117. *G. eureka.*

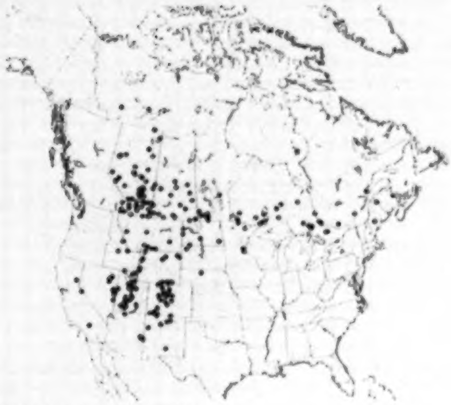


2-118. *G. brillians.*

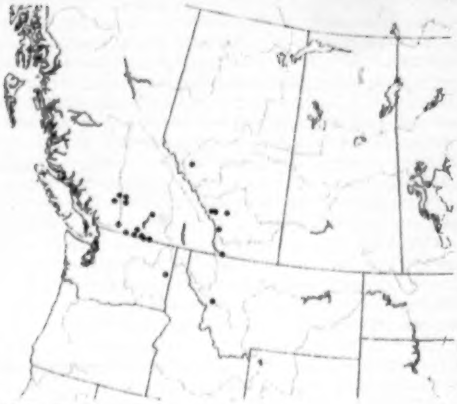


2-119. *G. bowmani.*

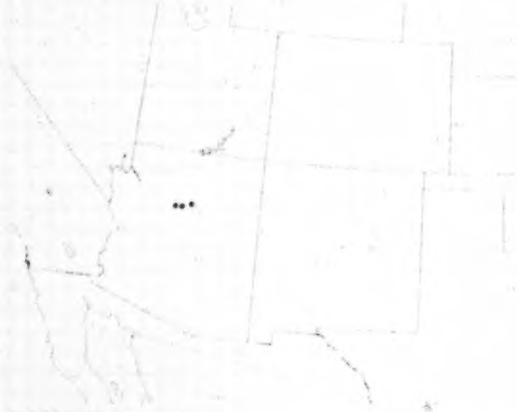
Figures 2-114 - 2-119. Distribution of examined specimens of *Grammia*.



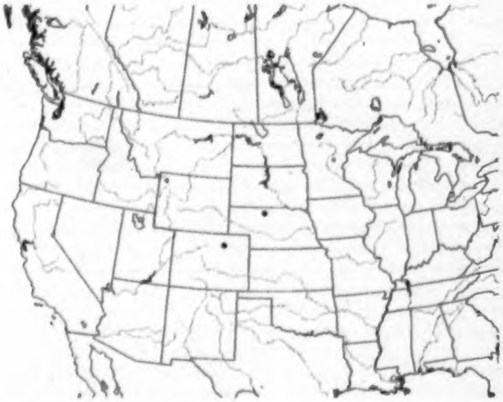
2-120. *G. williamsii.*



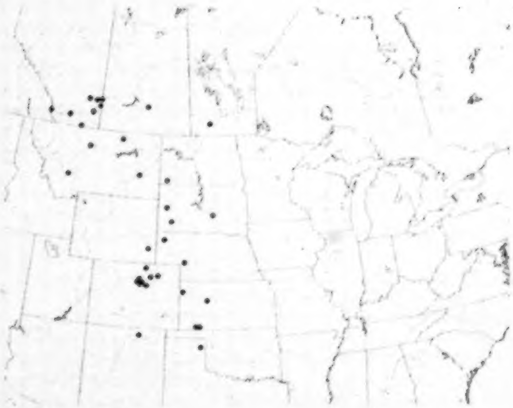
2-121. *G. elongata.*



2-122. *G. yavapai.*



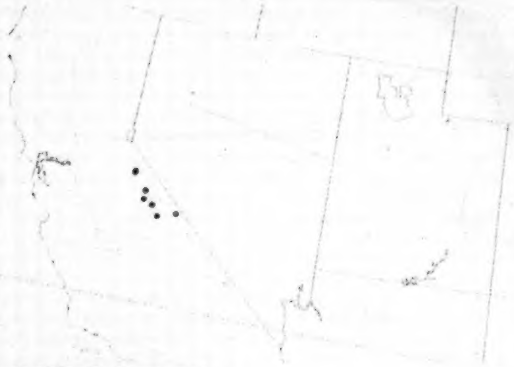
2-123. *G. favorita.*



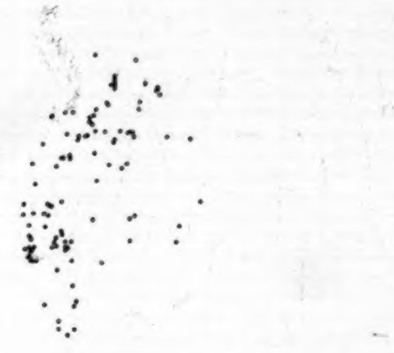
2-124. *G. blakei.*

2-125. *G. cervinoides.*

Figures 2-120 - 2-125. Distribution of examined specimens of *Grammia*.



2-126. *G. fergusoni.*



2-127. *G. ornata.*

2-128. *G. complicata.*

2-129. *G. hewletti.*

2-130. *G. bolanderi* .

2-131. *G. edwardsii.*

Figures 2-126 - 2-131. Distribution of examined specimens of *Grammia*.

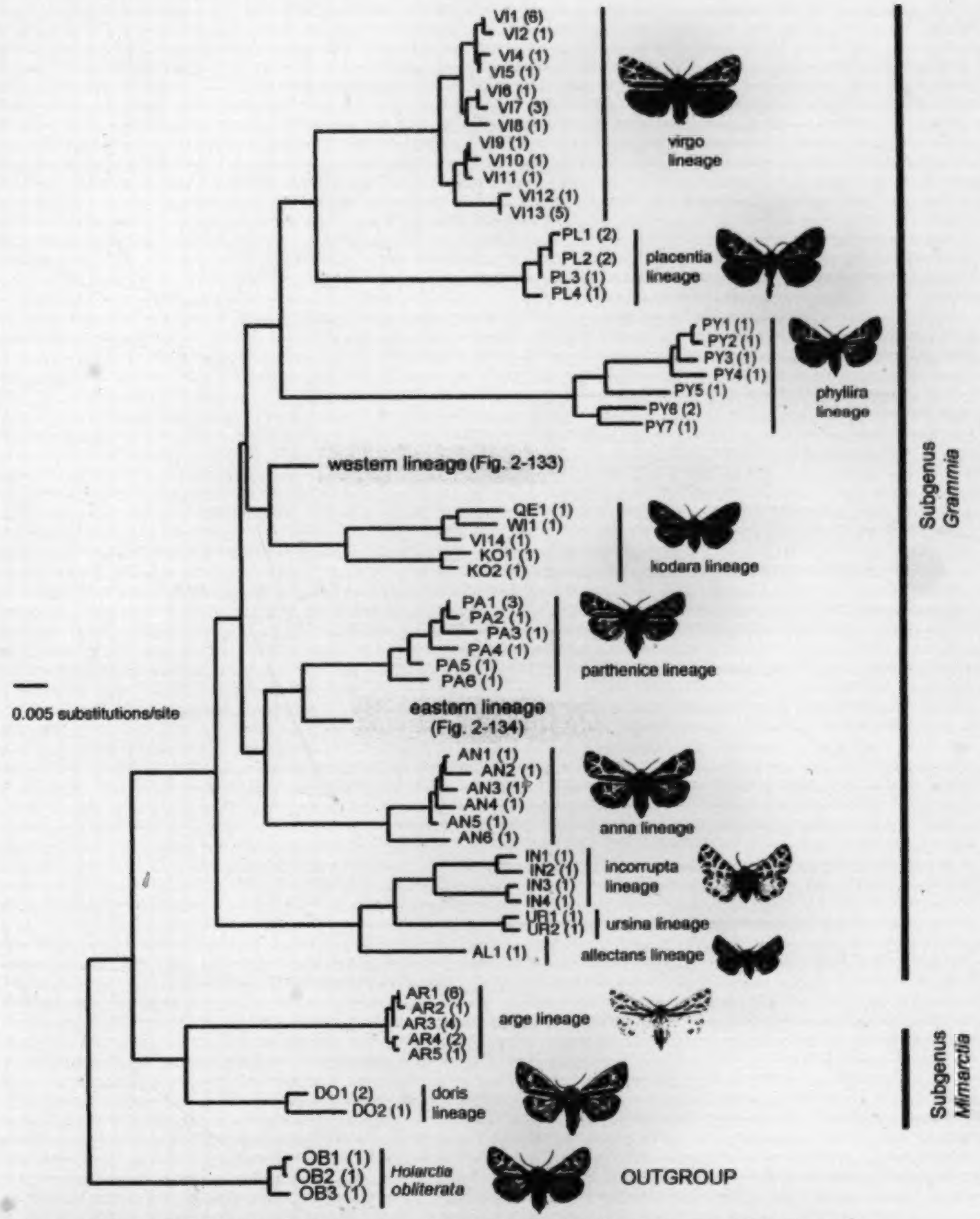

VI1 (6)
VI2 (1)
VI4 (1)
VI5 (1)
VI6 (1)
VI7 (3)
VI8 (1)
VI9 (1)
VI10 (1)
VI11 (1)
VI12 (1)
VI13 (5)
virgo lineage
PL1 (2)
PL2 (2)
PL3 (1)
PL4 (1)
placentia lineage
PY1 (1)
PY2 (1)
PY3 (1)
PY4 (1)
PY5 (1)
PY6 (2)
PY7 (1)
phyllira lineage
western lineage (Fig. 2-133)
QE1 (1)
WI1 (1)
VI14 (1)
KO1 (1)
KO2 (1)
kodara lineage
PA1 (3)
PA2 (1)
PA3 (1)
PA4 (1)
PA5 (1)
PA6 (1)
parthenice lineage
0.005 substitutions/site
eastern lineage (Fig. 2-134)
AN1 (1)
AN2 (1)
AN3 (1)
AN4 (1)
AN5 (1)
AN6 (1)
anna lineage
IN1 (1)
IN2 (1)
IN3 (1)
IN4 (1)
incorrupta lineage
UR1 (1)
UR2 (1)
ursina lineage
AL1 (1)
allectans lineage
AR1 (6)
AR2 (1)
AR3 (4)
AR4 (2)
AR5 (1)
arge lineage
DO1 (2)
DO2 (1)
doris lineage
OB1 (1)
OB2 (1)
OB3 (1)
Holoarctia obliterata
OUTGROUP
Subgenus Grammia
Subgenus Mimarctia

Figure 2-132. Neighbour-joining tree of *cox1* 'barcode' haplotypes of *Holoarctia obliterata* and *Grammia* species. Two-letter codes correspond to the species name in a given lineage. The Kodara Lineage includes *G. quenseli* (QE1), *G. williamsii* (WI1), and *G. virgo* (VI14) haplotypes. Haplotypes of the Western and Eastern lineages are shown separately in Figures 2-133 and 2-134, respectively. Numbers in parentheses indicate number of specimens.

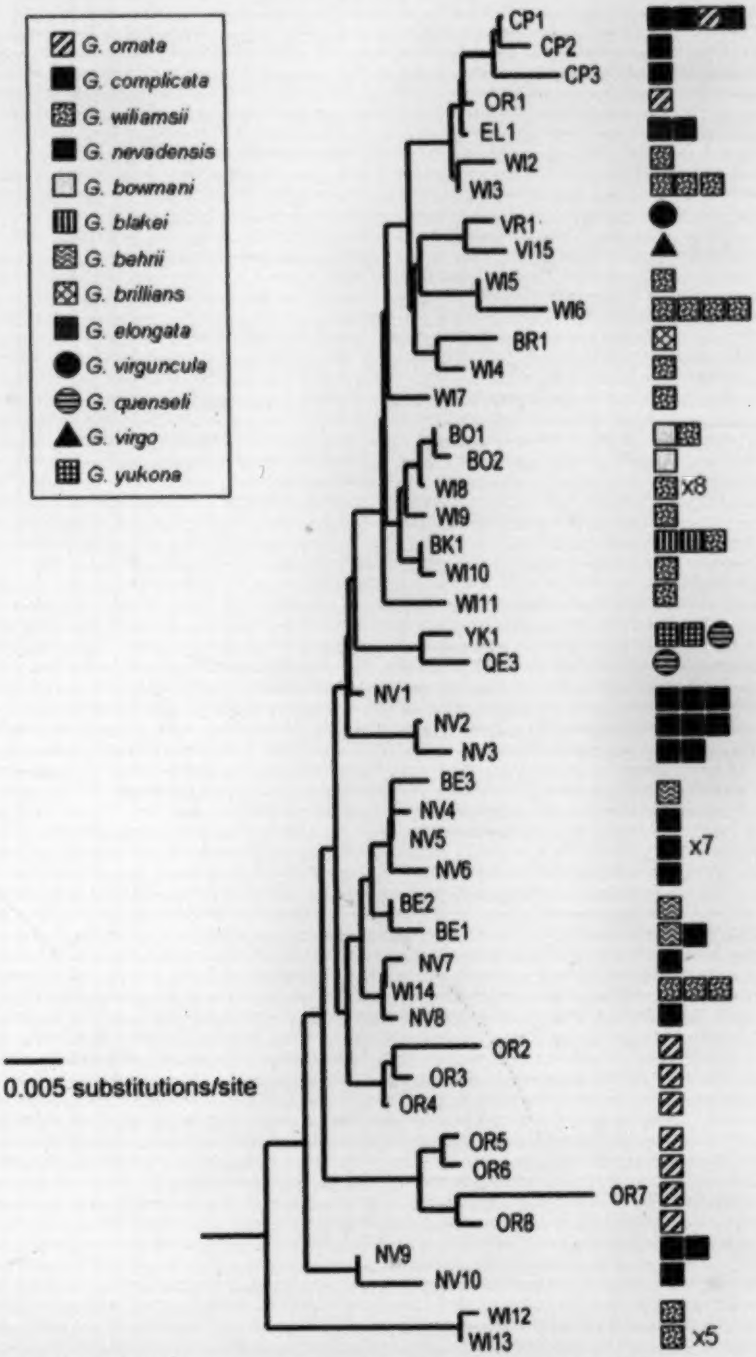

G. ornata
G. complicata
G. wiliamsii
G. nevadensis
G. bowmani
G. blakei
G. behrii
G. brillians
G. elongata
G. virguncula
G. quenseli
G. virgo
G. yukona
CP1
CP2
CP3
OR1
EL1
WI2
WI3
VR1
VI15
WI5
WI6
BR1
WI4
WI7
BO1
BO2
WI8
WI9
BK1
WI10
WI11
YK1
QE3
NV1
NV2
NV3
BE3
NV4
NV5
NV6
BE2
BE1
NV7
WI14
NV8
OR2
OR3
OR4
OR5
OR6
OR7
OR8
NV9
NV10
WI12
WI13
x8
x7
x5
0.005 substitutions/site

Figure 2-133. Neighbour-joining tree of Western lineage haplotypes of *Grammia* species. Multiple symbols per row indicate multiple samples for a given haplotype. Squares indicate species with haplotype compliments primarily or exclusively in the Western lineage, circles indicate predominantly Eastern lineage species. *Grammia virgo* haplotype VI15 (triangle) is the sole *G. virgo* haplotype outside of the Virgo lineage.

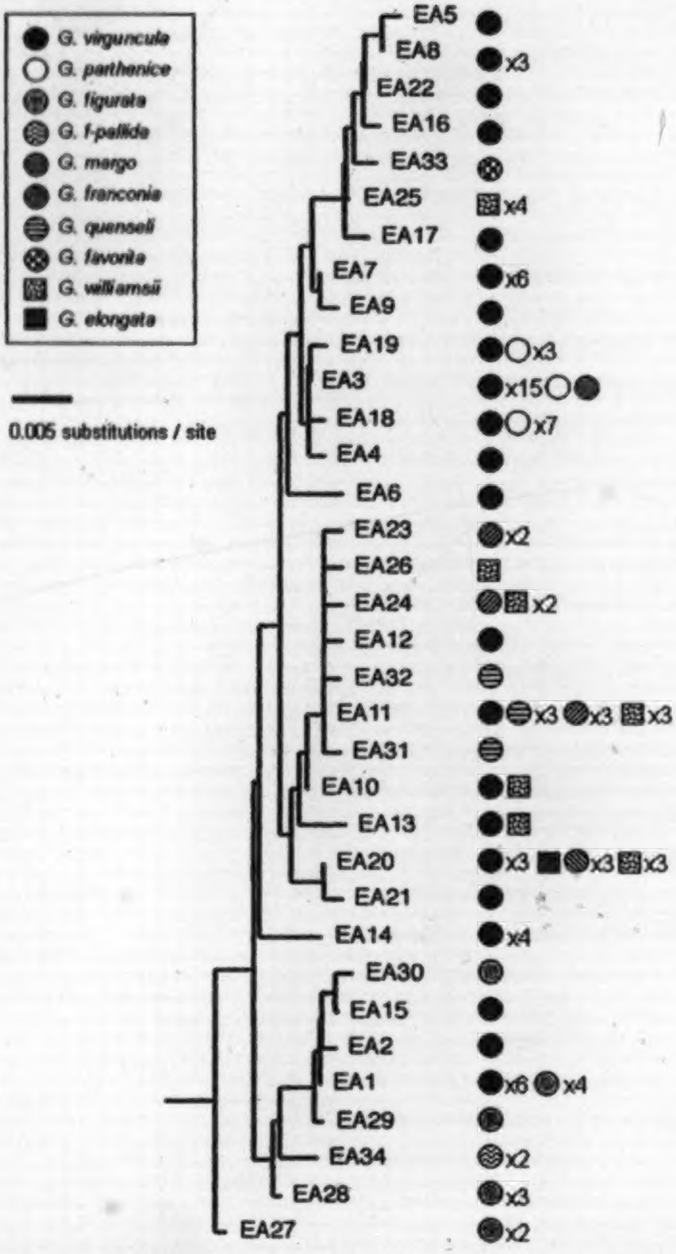

G. virguncula
G. parthenice
G. figurata
G. f-pallida
G. margo
G. franconia
G. quenseli
G. favorita
G. williamsii
G. elongata
0.005 substitutions / site
EA5
EA8 x3
EA22
EA16
EA33
EA25 x4
EA17
EA7 x6
EA9
EA19 x3
EA3 x15
EA18 x7
EA4
EA6
EA23 x2
EA26
EA24 x2
EA12
EA32
EA11 x3 x3 x3
EA31
EA10
EA13
EA20 x3 x3 x3
EA21
EA14 x4
EA30
EA15
EA2
EA1 x6 x4
EA29
EA34 x2
EA28 x3
EA27 x2

Figure 2-134. Neighbour-joining tree of Eastern lineage haplotypes of *Grammia* species. Multiple symbols per row indicate multiple samples of a given haplotype. Circles indicate primarily or exclusively Eastern clade species, squares indicate species with haplotype compliments primarily in the Western clade.

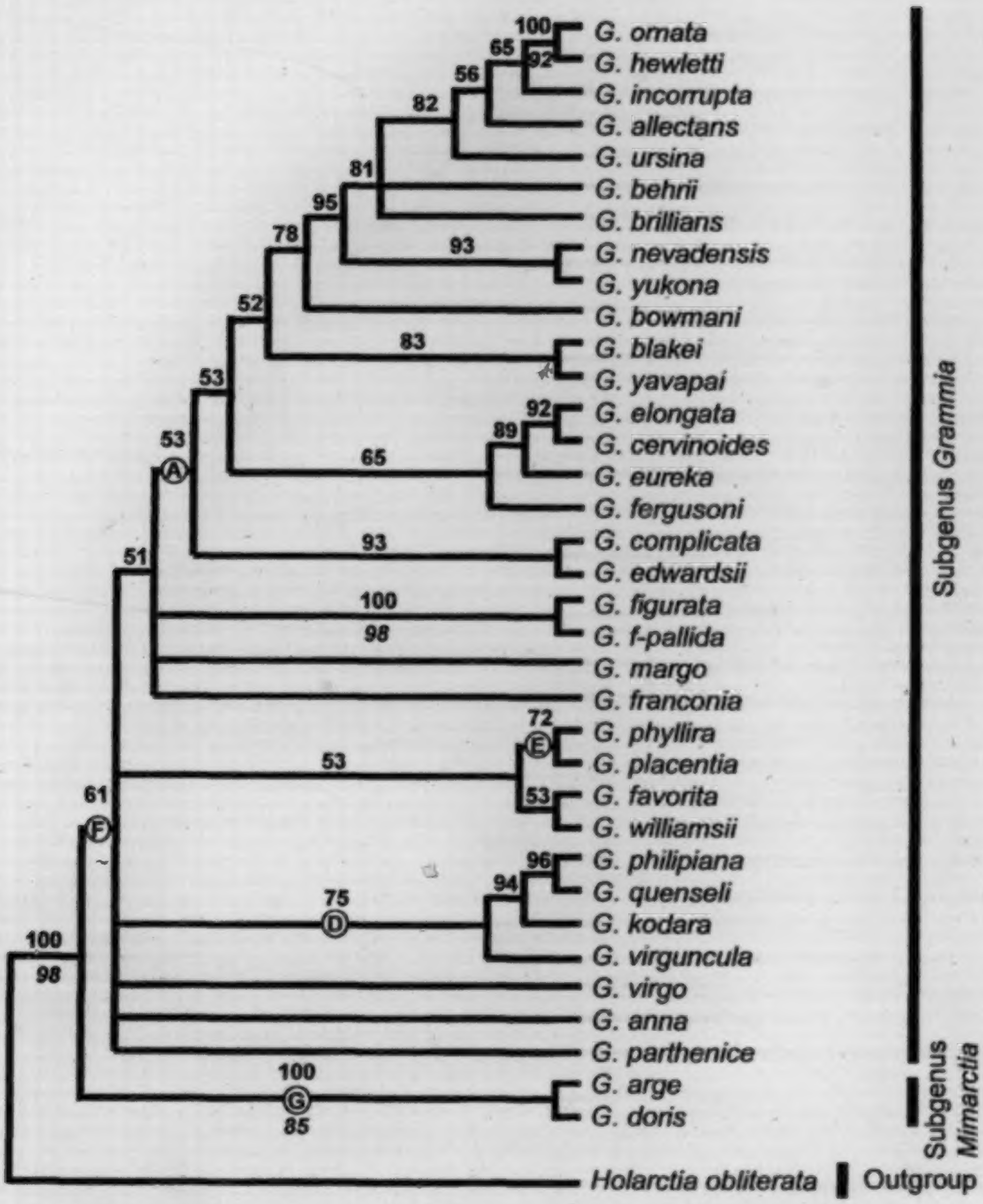

100
G. ornata
65
92
G. hewletti
56
G. incorrupta
82
G. allectans
G. ursina
81
G. behrii
95
G. brillians
78
93
G. nevadensis
G. yukona
52
G. bowmani
83
G. blakei
53
G. yavapai
92
G. elongata
53
89
G. cervinoides
A
65
G. eureka
G. fergusoni
93
G. complicata
51
G. edwardsii
100
G. figurata
98
G. f-pallida
G. margo
G. franconia
72
G. phyllira
E
53
G. placentia
61
53
G. favorita
F
G. williamsii
96
G. philipiana
94
G. quenseli
75
D
G. kodara
100
G. virguncula
98
G. virgo
G. anna
G. parthenice
100
G. arge
G
85
G. doris
Holarctia obliterata
Outgroup
Subgenus Grammia
Subgenus Mimarctia

Figure 2-135. Maximum parsimony cladogram of 35 *Grammia* species based on 43 morphological characters, shown as a majority-rule consensus of 100,515 most-parsimonious trees. Values above and below internal branches indicate majority rule frequencies and bootstrap support values greater than 50%, respectively. Lettered clades refer to those discussed in the text. Tree length = 97, Consistency Index = 0.45, Retention Index = 0.769.

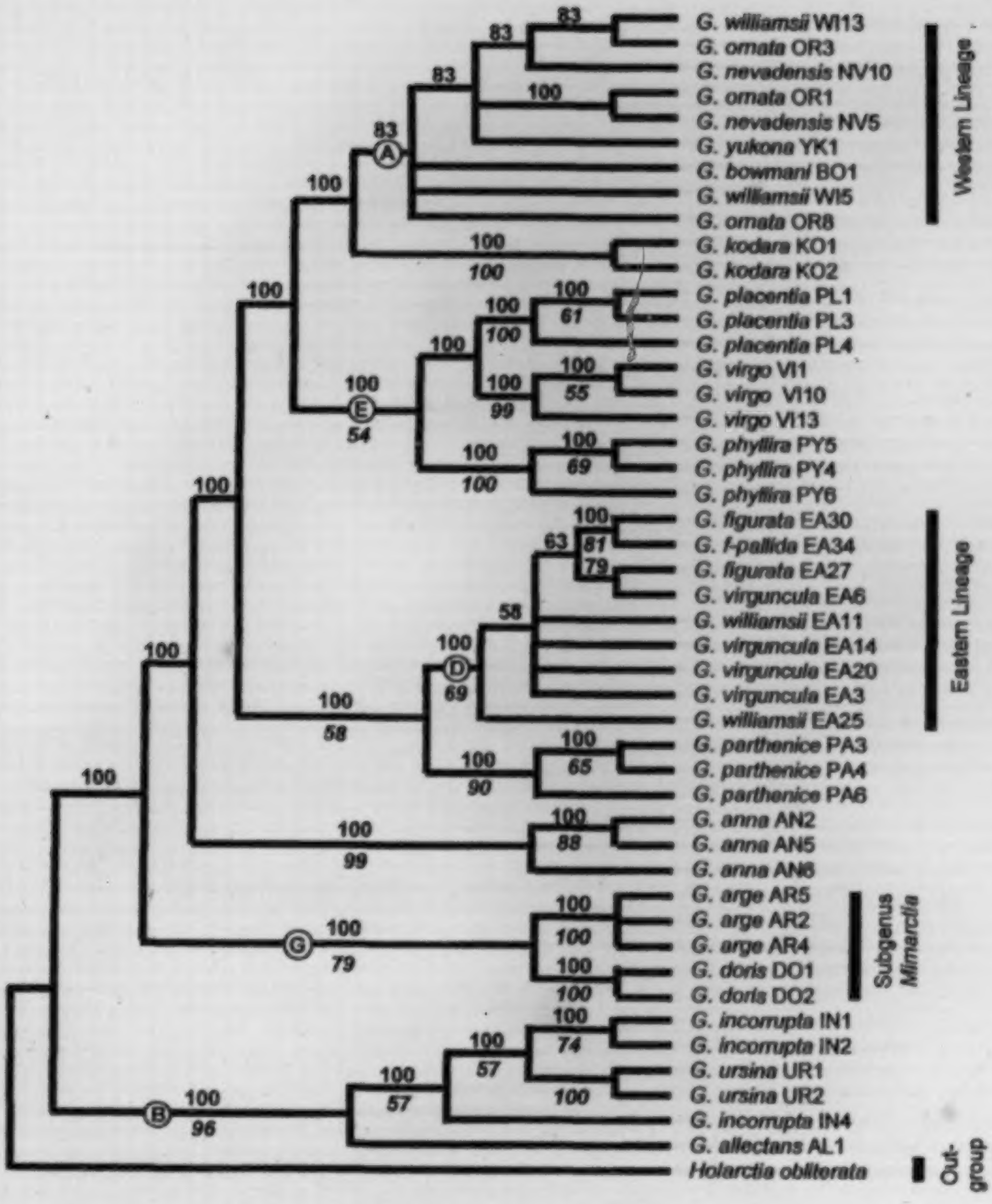

G. williamsii WI13
G. ornata OR3
G. nevadensis NV10
G. ornata OR1
G. nevadensis NV5
G. yukona YK1
G. bowmani BO1
G. williamsii WI5
G. ornata OR8
G. kodara KO1
G. kodara KO2
G. placentia PL1
G. placentia PL3
G. placentia PL4
G. virgo VI1
G. virgo VI10
G. virgo VI13
G. phyllira PY5
G. phyllira PY4
G. phyllira PY6
G. figurata EA30
G. f-pallida EA34
G. figurata EA27
G. virguncula EA6
G. williamsii EA11
G. virguncula EA14
G. virguncula EA20
G. virguncula EA3
G. williamsii EA25
G. parthenice PA3
G. parthenice PA4
G. parthenice PA6
G. anna AN2
G. anna AN5
G. anna AN6
G. arge AR5
G. arge AR2
G. arge AR4
G. doris DO1
G. doris DO2
G. incorrupta IN1
G. incorrupta IN2
G. ursina UR1
G. ursina UR2
G. incorrupta IN4
G. allectans AL1
Holarctia obliterata
Western Lineage
Eastern Lineage
Subgenus Mimarctia
Out-group
A
E
D
G
B

Figure 2-136. Maximum parsimony cladogram of *Grammia* species, based on subsample of all *cox1* haplotype lineages shown in Fig. 2-132 (see text for subsampling criteria). Shown is the majority-rule consensus of 912 most-parsimonious trees, based on the 658 base-pair 'barcode' region. Values above and below internal branches indicate majority rule frequencies and bootstrap support values greater than 50%, respectively. Lettered clades indicate those discussed in the text. Tree length = 481, Consistency Index = 0.449, Retention Index = 0.749.

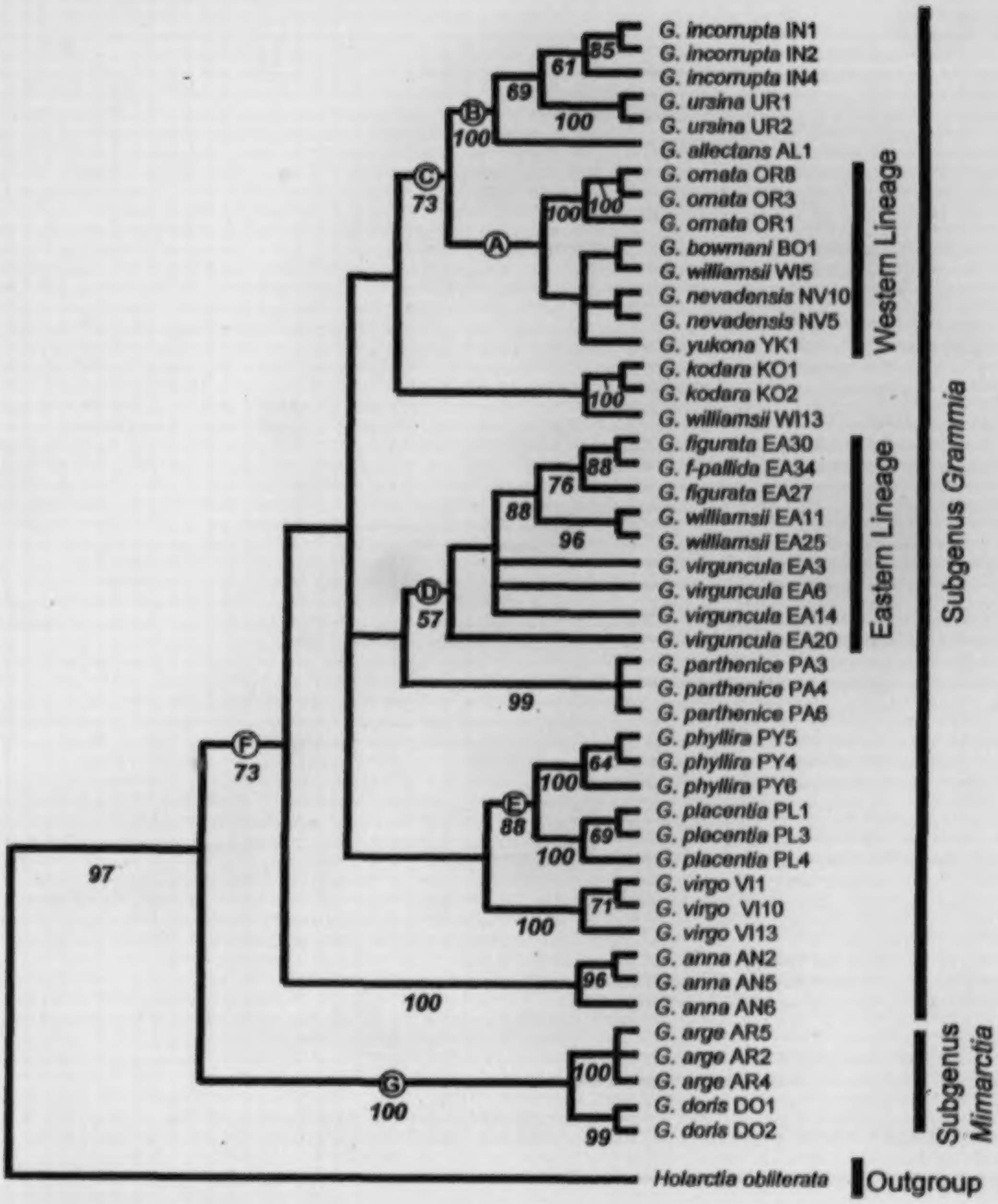

G. incorrupta IN1
G. incorrupta IN2
G. incorrupta IN4
G. ursina UR1
G. ursina UR2
G. allectans AL1
G. ornata OR8
G. ornata OR3
G. ornata OR1
G. bowmani BO1
G. williamsii WI5
G. nevadensis NV10
G. nevadensis NV5
G. yukona YK1
G. kodara KO1
G. kodara KO2
G. williamsii WI13
G. figurata EA30
G. f-pallida EA34
G. figurata EA27
G. williamsii EA11
G. williamsii EA25
G. virguncula EA3
G. virguncula EA6
G. virguncula EA14
G. virguncula EA20
G. parthenice PA3
G. parthenice PA4
G. parthenice PA6
G. phyllira PY5
G. phyllira PY4
G. phyllira PY6
G. placentia PL1
G. placentia PL3
G. placentia PL4
G. virgo VI1
G. virgo VI10
G. virgo VI13
G. anna AN2
G. anna AN5
G. anna AN6
G. arge AR5
G. arge AR2
G. arge AR4
G. doris DO1
G. doris DO2
Holarctia obliterata
Western Lineage
Eastern Lineage
Subgenus Grammia
Subgenus Mimarctia
Outgroup
A
B
C
D
E
F
G
85
61
69
100
100
100
100
73
100
88
76
88
96
57
99
64
100
88
69
100
71
100
73
96
100
97
100
100
99

Figure 2-137. Maximum parsimony cladogram of *Grammia* species based on combined morphology and *cox1* 'barcode' datasets. Shown is the strict consensus of 16 most-parsimonious trees. Values below internal branches indicate bootstrap support values greater than 50%. Lettered clades indicate those discussed in the text. Tree length = 585, Consistency Index = 0.442, Retention Index = 0.761.

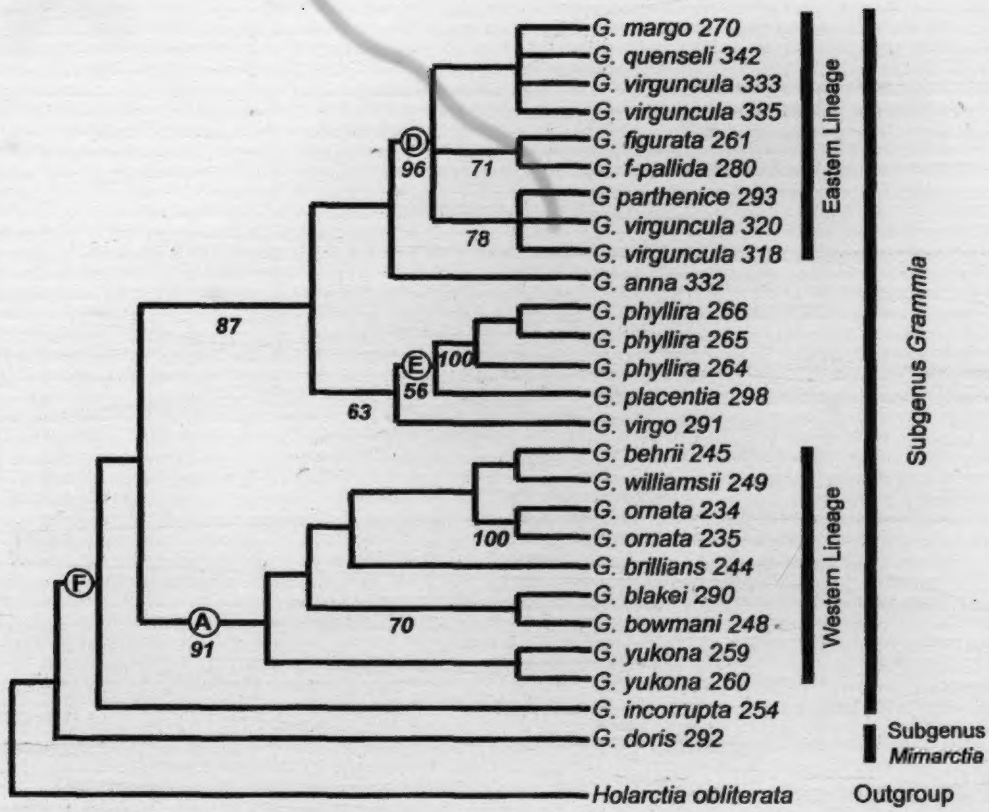

G. margo 270
G. quenseli 342
G. virguncula 333
G. virguncula 335
G. figurata 261
G. f-pallida 280
G parthenice 293
G. virguncula 320
G. virguncula 318
G. anna 332
G. phyllira 266
G. phyllira 265
G. phyllira 264
G. placentia 298
G. virgo 291
G. behrii 245
G. williamsii 249
G. ornata 234
G. ornata 235
G. brillians 244
G. blakei 290
G. bowmani 248
G. yukona 259
G. yukona 260
G. incorrupta 254
G. doris 292
Holarctia obliterata
Eastern Lineage
Western Lineage
Subgenus Grammia
Subgenus Mimarctia
Outgroup
D
96
71
78
87
E
100
56
63
100
70
A
91
F

Figure 2-138. Maximum parsimony cladogram of 19 *Grammia* species based on combined morphological characters and 'barcode'+ 'Jerry-Pat' *cox1* sequence. Shown is the strict consensus of 8 most-parsimonious trees. Values below internal branches indicate bootstrap support values greater than 50%. Tree length = 894, Consistency Index = 0.496, Retention Index = 0.701. Lettered clades are referred to in the text, Specimen numbers correspond to "BCSC___" numbers in Appendix 2-1.

Appendix 2-1. Data for morphology and molecular sequence voucher specimens.

cox1 'barcode' haplotype	Clade	Identification	Locality	Collector	Date	Voucher Depostion*	Specimen/ Sample ID	Dissection voucher	GenBank Accession No. **	No. bp *cox1*
AL1	allectans	*Grammia allectans*	USA: AZ: Cochise Co., Chiracahuah Mtns.	Walsh, B.	21-Jun-2001	BCSC	BCSC246	x	EU119423	658
-	-	*Grammia anna*	CAN: ON: Carp Ridge	Troubridge, J.T.	16-Jun-2004	BCSC	CS3169	x	-	-
-	-	*Grammia anna*	USA: PA: Lackawanna Co, 3 mi E Archbald	Johnson, S.	26-Jun-2001	BCSC	CS_3009	x	-	-
AN1	anna	*Grammia anna*	CAN: QC: Pontiac, Chutes de Luskville	Handfield, D.	10-Jun-2005	DHC	DH010643	-	EU119600	658
AN2	anna	*Grammia anna*	USA: NC: Macon Co., Slick Rock	Adams, J. K.	21-May-2000	BIO	06-JKA-0005	-	n/a	658
AN3	anna	*Grammia anna*	CAN: ON: Carp	Troubridge, J. T.	28-Jun-2003	BCSC	BCSC332	-	EU119424	1357
AN4	anna	*Grammia anna*	USA: GA: Walker Co., Taylor's Ridge	Adams, J. K.; Finkelstein, I.	23-Apr-2006	BIO	06-JKA-0396	-	n/a	622
AN5	anna	*Grammia anna*	USA: NC: Macon Co., Little Scaly Mtn.	Adams, J. K.	21-May-2000	BIO	06-JKA-0004	-	n/a	580
AN6	anna	*Grammia anna*	USA: GA: Walker Co., Taylor's Ridge	Adams, J. K.; Finkelstein, I.	23-Apr-2006	BIO	06-JKA-0395	-	n/a	658
-	-	*Grammia arge*	USA: KY: Morehead		27-Jun-1962	CNC	CS3180	x	-	-
-	-	*Grammia arge*	CAN: ON: Canfield, 3 mi S	Troubridge, J.	24-May-1988	UASM	CS3181	x	-	-
AR1	arge	*Grammia arge*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	04-Sep-2005	BIO	2005-ONT-1894	-	n/a	658
AR1	arge	*Grammia arge*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	23-Jul-2005	BIO	2005-ONT-667	-	n/a	658
AR1	arge	*Grammia arge*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	26-Jul-2005	BIO	2005-ONT-762	-	n/a	658
AR1	arge	*Grammia arge*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	28-Jul-2005	BIO	2005-ONT-816	-	n/a	658
AR1	arge	*Grammia arge*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	28-May-2006	BIO	2006-ONT-0402	-	n/a	658
AR1	arge	*Grammia arge*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	15-Apr-2003	BIO	Moth4625.03	-	n/a	572
AR2	arge	*Grammia arge*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	?	BIO	APAN1.01	-	AF549622	617
AR3	arge	*Grammia arge*	USA: NC: Alleghany Co., New River SP	Sullivan, J. B.	04-Sep-2002	BIO	06-NCNW-0015	-	EU119601	656

Appendix 2-1 (cont'd.). Data for morphology and molecular sequence voucher specimens.

' *cox1* 'barcode' haplotype	Clade	Identification	Locality	Collector	Date	Voucher Depostion*	Specimen/ Sample ID	Dissection voucher	GenBank Accession No. **	No. bp *cox1*
AR3	arge	*Grammia arge*	USA: NC: Alleghany Co., New River SP	Sullivan, J. B.	04-Sep-2002	BIO	06-NCNW-0016	-	EU119602	657
AR3	arge	*Grammia arge*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	28-Jul-2005	BIO	2005-ONT-817	-	n/a	628
AR3	arge	*Grammia arge*	CAN: ON: Carp	Troubridge, J. T.	18-Aug-2003	BCSC	BCSC239	-	EU119425	658
AR4	arge	*Grammia arge*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	24-Jul-2005	BIO	2005-ONT-685	-	n/a	658
AR4	arge	*Grammia arge*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	29-Jul-2005	BIO	2005-ONT-836	-	n/a	658
AR5	arge	*Grammia arge*	USA: PA: Pillow	Johnson, S.	21-Sep-1995	BCSC	BCSC238	-	EU119426	658
-	-	*Grammia behrii*	USA: CA: Kern Co., Lebec	Sala, F.	03-Sep-1944	LACM	CS3163	x	-	-
-	-	*Grammia behrii*	USA: CA: Los Angeles Co., Mint Cyn.			LACM	CS3190	x	-	-
-	-	*Grammia behrii*	USA: CA: Plumas Co., Jackson Ck.	Troubridge, J.T.	28-Aug-2000	UASM	CS_3247	x	-	-
-	-	*Grammia behrii*	USA: CA: Los Angeles Co., Escondido Summit, Mint Cyn area	Sala, F.	20-Jul-1969	USNM	CS_3251	x	-	-
BE1	western	*Grammia behrii*	USA: OR: Josephine Co., Eight $ Mtn.	Troubridge, J. T.	29-Aug-2002	CNC	CNCNoctuoidea 10182	-	EU119604	658
BE2	western	*Grammia behrii*	USA: OR: Josephine Co., Eight $ Mtn.	Troubridge, J. T.	29-Aug-2002	CNC	CNCNoctuoidea 10181	-	EU119603	658
BE3	western	*Grammia behrii*	USA: OR: Josephine Co., Eight $ Mtn.	Troubridge, J. T.	27-Aug-2002	CNC	BCSC245	-	EU119427	1357
-	-	*Grammia blakei*	CAN: AB: Jenner, 10km N	Schmidt, C.; Anweiler, G.	03-Jun-2004	UASM	CS3043	x	-	-
-	-	*Grammia blakei*	CAN: AB: Jenner, 10km N	Schmidt, C.; Anweiler, G.	03-Jun-2004	UASM	CS3182	x	-	-
-	-	*Grammia blakei*	CAN: AB: Medicine Hat		18-Jun-1928	CNC	CS3044	x	-	-
BK1	western	*Grammia blakei*	CAN: AB: Cavendish, 2km S	Schmidt, B. C.	03-Jun-2004	UASM	BCSC290	-	EU119429	1357
BK1	western	*Grammia blakei*	CAN: AB: Jenner, 10km N	Schmidt, B. C.; Anweiler, G.	03-Jun-2004	UASM	BCSC230	-	EU119428	658
-	-	*Grammia bowmani*	USA: CO: Mesa Co., Colo. Nat. Mon, Upper No Thoroughfare Cyn.	Rodgers, B.	18-Jun-1996	BCSC	CS_3024	x	-	-
-	-	*Grammia bowmani*	USA: CO: Mesa Co., Black Ridge	Bowman, D.		OPLER	USNM59071	x	-	-
-	-	*Grammia bowmani*	USA: CO: Mesa Co., Black Ridge	Bowman, D.		OPLER	USNM60102	x	-	-

Appendix 2-1 (cont'd.). Data for morphology and molecular sequence voucher specimens.

cox1 'barcode' haplotype	Clade	Identification	Locality	Collector	Date	Voucher Depostion*	Specimen/ Sample ID	Dissection voucher	GenBank Accession No. **	No. bp *cox1*
BO1	western	*Grammia bowmani*	USA: CO: Mesa Co., Colorado NM	Opler, P.	07-Jun-2000	BCSC	BCSC247	-	EU119430	657
BO2	western	*Grammia bowmani*	USA: CO: Mesa Co., Colorado NM	Moore, J.	03-Jul-2001	BCSC	BCSC248	-	EU119431	1357
-	-	*Grammia brillians*	USA: UT: Garfield Co., Bryce Cyn. NP, Water Cyn. 6800'	Mueller, S.	10-Jul-2005	USNM	CS3038	x	-	-
BR1	western	*Grammia brillians*	USA: UT: Bryce Cyn.	Mueller, S.	10-Jul-2005	CNC	BCSC244	-	EU119500	1357
-	-	*Grammia cervinoides*	USA: CO: Park Co., Pennsylvania Mtn. 3930m	Ford, D.	21-Jul-1980	CNC	CS3042	x	-	-
-	-	*Grammia complicata*	CAN: BC: Saanich, Bracfoot[?]	Hardy, G.	29-Jun-1954	RBCM	CS3187	x	-	-
-	-	*Grammia complicata*	CAN: BC: Saanich, Mt. Douglas	Burbridge, J.	25-Mar-1934	RBCM	CS3157	x	-	-
-	-	*Grammia complicata*	CAN: BC: Saanich, Mt. Douglas	Burbridge, J.	25-Mar-1934	RBCM	CS3189	x	-	-
-	-	*Grammia complicata*	CAN: BC: Victoria		17-Jul-1900	RBCM	CS3161	x	-	-
-	-	*Grammia complicata*	CAN: BC: Victoria			RBCM	CS3186	x	-	-
CP1	western	*Grammia complicata*	CAN: BC: Goose Spit	Page, N.	04-Jun-2003	CNC	CNCNoctuoidea 10226	-	EU119611	658
CP1	western	*Grammia complicata*	CAN: BC: Savary Island	Page, N.	11-Jun-2002	CNC	BCSC232	-	EU119435	658
CP2	western	*Grammia complicata*	CAN: BC: Sandy Island	Woodward, D.	08-Jun-2000	CNC	BCSC231	-	EU119433	658
CP3	western	*Grammia complicata*	USA: WA: Pacific Co., Long Beach	Troubridge, J. T.	24-Jul-1997	CNC	BCSC233	-	EU119434	597
-	-	*Grammia doris*	CAN: BC: Osoyoos		n.d.	CNC	ARCT1042	x	-	-
-	-	*Grammia doris*	USA: SC: Berkeley Co., McClellanville, Wedge			CNC	CS3178	x	-	-
-	-	*Grammia doris*	USA: SC: Berkeley Co., McClellanville, Wedge			CNC	CS3179	x	-	-
DO1	doris	*Grammia doris*	CAN: AB: Deadwood, 21km E	Bone, S.	10-Jun-2003	BCSC	BCSC236	-	EU119438	658
DO1	doris	*Grammia doris*	CAN: AB: Peace River	Hood, B.	16-Jun-2004	BCSC	BCSC237	-	EU119437	658
DO2	doris	*Grammia doris*	USA: FL: Putnam Co.	Slotten, J.	28-Jul-2003	BCSC	BCSC292	-	EU119436	1357
-	-	*Grammia elongata*	CAN: BC: Cache Creek, Cornwall Hills summit area	Guppy, C. S.	03-Aug-1988	tish Columbia	BCSC251	x	-	-
-	-	*Grammia elongata*	CAN: AB: Mount Allan, Kananaskis	Pike, E. M.	14-Jun-1990	UASM	UASM35932	x	-	-
-	-	*Grammia elongata*	CAN: AB: Prospect Mtn.	Pike, E. M.	21-Jul-1979	UASM	UASM35937	x	-	-
CP1	western	*Grammia elongata*	CAN: BC: Cathedral PP, Glacier L.	Cannings, S. G.	24-Jul-1988	RBCM	BCSC384	-	EU119441	584
EA20	eastern	*Grammia elongata*	CAN: AB: Bragg Creek, 22km W	Schmidt, B. C.	23-Jul-2001	BCSC	BCSC392	-	EU119442	658

Appendix 2-1 (cont'd.). Data for morphology and molecular sequence voucher specimens.

cox1 'barcode' haplotype	Clade	Identification	Locality	Collector	Date	Voucher Depostion*	Specimen/ Sample ID	Dissection voucher	GenBank Accession No. **	No. bp *cox1*
EL1	western	*Grammia elongata*	CAN: AB: Bragg Creek, 22km W	Schmidt, B. C.	27-Jul-1998	BCSC	BCSC252	-	EU119439	658
EL1	western	*Grammia elongata*	CAN: BC: Cache Creek, Cornwall Hills	Guppy, C. S.	03-Aug-1988	RBCM	BCSC251	-	EU119440	517
-	-	*Grammia eureka*	USA: UT: Juab Co., Eureka	Spalding, T.	09-May-1910	USNM	USNM56401	x	-	-
-	-	*Grammia favorita*	USA: NE: Cherry Co., Valentine NWR, Hackberry L.	Ferguson, D.	15-Jun-1983	CNC	CS3175	x	-	-
EA33	eastern	*Grammia favorita*	USA: CO: Weld Co., Roggen	Bowman, D.	15-May-1993	USNM	BCSC262	-	EU119443	587
-	-	*Grammia fergusoni*	USA: CA: Tuolumne Co., Leavitt Peak 11050 - 12000'	Opler, P.	29-Aug-1967	BERK	CS3040	x	-	-
-	-	*Grammia fergusoni*	USA: CA: Mono Co., Tioga Pass	Andrews & Martin	03-Aug-1935	LACM	CS3162	x	-	-
-	-	*Grammia figurata*	CAN: ON: Backus Woods, St. Williams	Troubridge, J.T.	14-Jun-2003	TROU	CS_3012	x	-	-
EA1	eastern	*Grammia figurata*	CAN: ON: St. Williams	Troubridge, J. T.	14-Jun-2003	CNC	BCSC268	-	EU119448	658
EA1	eastern	*Grammia figurata*	CAN: ON: St. Williams	Troubridge, J. T.	14-Jun-2003	CNC	CNCNoctuoidea 10073	-	EU119614	613
EA1	eastern	*Grammia figurata*	CAN: ON: St. Williams	Troubridge, J. T.	14-Jun-2003	CNC	CNCNoctuoidea 10144	-	EU119612	658
EA1	eastern	*Grammia figurata*	CAN: ON: St. Williams	Troubridge, J. T.	16-Jun-2005	CNC	CNCNoctuoidea 6650	-	EU119616	658
EA27	eastern	*Grammia figurata*	USA: CT: Hartford Co., East Hartford	-	03-Jun-2005	BIO	05-CTATBI-0021	-	n/a	618
EA27	eastern	*Grammia figurata*	USA: PA: Northumberland	Johnson, S.	02-Jun-1995	BCSC	BCSC282	-	EU119444	604
EA28	eastern	*Grammia figurata*	USA: IL: Jackson Co.	Lawrie, D.	22-May-2001	BCSC	BCSC297	-	EU119447	573
EA28	eastern	*Grammia figurata*	USA: OK: Oklahoma Co., Luther	Harp, C.	20-Aug-1990	BCSC	BCSC281	-	EU119446	585
EA28	eastern	*Grammia figurata*	USA: PA: 1.2 mi S Nottingham	Johnson, S.	29-May-2004	BCSC	BCSC261	-	EU119449	1357
EA29	eastern	*Grammia figurata*	USA: KS: Trego Co., Cedar Bluff St. Pk.	Landry, J. F. & B	12-Jul-1989	CNC	BCSC391	-	EU119445	658
EA30	eastern	*Grammia figurata*	CAN: ON: St. Williams	Troubridge, J. T.	18-Jun-2005	CNC	CNCNoctuoidea 6649	-	EU119615	658
-	-	*Grammia f-pallida*	USA: CO: Boulder Co., Boulder			CNC	ARCT1068	x	-	-
-	-	*Grammia f-pallida*	USA: TX: Jeff Davis Co., Davis Mtns Resort 5800'	Marqua, D. G.	25-May-1990	LACM	CS3164	x	-	-
EA34	eastern	*Grammia f-pallida*	USA: CO: Baca Co., Comanche NG	Pogue, M.; Harp, C.	25-Aug-2004	BCSC	BCSC279	-	EU119452	658

Appendix 2-1 (cont'd.). Data for morphology and molecular sequence voucher specimens.

cox1 'barcode' haplotype	Clade	Identification	Locality	Collector	Date	Voucher Depostion*	Specimen/ Sample ID	Dissection voucher	GenBank Accession No. **	No. bp *cox1*
EA34	eastern	*Grammia f-pallida*	USA: OK: Cimarron Co., Black Mesa SP	Pogue, M.; Harp, C.	24-Aug-2004	BCSC	BCSC280	-	EU119460	1357
-	-	*Grammia franconia*	CAN: ON: Bobcaygeon		02-Jun-1931	CNC	CS3165	x	-	-
-	-	*Grammia franconia*	CAN: ON: Frontenac Co., Perth Rd.	Ward, P.	09-Jun-1970	CNC	CS_3010	x	-	-
EA11	eastern	*Grammia franconia*	CAN: ON: Carp	Troubridge, J. T.	19-Jun-2004	CNC	CNCNoctuoidea 10074	-	EU119605	583
EA11	eastern	*Grammia franconia*	CAN: ON: Carp	Troubridge, J. T.	06-Jun-2004	CNC	CNCNoctuoidea 10075	-	EU119606	615
EA11	eastern	*Grammia franconia*	CAN: QC: St-Michel des Saints	Handfield, D.	29-Jun-2005	DHC	DH010296	-	EU119608	658
EA23	eastern	*Grammia franconia*	CAN: ON: Carp	Troubridge, J. T.	23-Jun-2003	CNC	BCSC385	-	EU119509	658
EA23	eastern	*Grammia franconia*	CAN: ON: Carp	Troubridge, J. T.	09-Jun-2003	CNC	CNCNoctuoidea 10134	-	EU119609	658
EA24	eastern	*Grammia franconia*	CAN: QC: St-Michel des Saints	Handfield, D.	29-Jun-2005	DHC	DH010295	-	EU119607	658
-	-	*Grammia hewletti*	USA: CA: San Diego Co., 3mi E Julian	Bloomfield, N.	14-Jun-1998	BERK	CS3160	x	-	-
-	-	*Grammia hewletti*	USA: CA: San Diego Co., Nellie			CNC	ARCT1060	x	-	-
-	-	*Grammia incorrupta*	USA: AZ: Pima Co, mi. 11 Mt Lemmon Hwy, 5800'	Walsh, B.	03-Jun-2004	BCSC	CS_3022	x	-	-
-	-	*Grammia incorrupta*	USA: AZ: Pima Co, mi. 11 Mt Lemmon Hwy, 5800'	Walsh, B.	03-Jun-2004	BCSC	CS_3231	x	-	-
-	-	*Grammia incorrupta*	USA: AZ: Pima Co, mi. 11 Mt Lemmon Hwy, 5800'	Walsh, B.	03-Jun-2004	BCSC	CS_3252	x	-	-
-	-	*Grammia incorrupta*	USA: AZ: Pima Co, mi. 11 Mt Lemmon Hwy, 5800'	Walsh, B.	03-Jun-2004	BCSC	CS_3253	x	-	-
-	-	*Grammia incorrupta*	USA: AZ: Pima Co, mi. 11 Mt Lemmon Hwy, 5800'	Walsh, B.	03-Jun-2004	BCSC	CS_3254	x	-	-
-	-	*Grammia incorrupta*	USA: AZ: Pima Co, mi. 11 Mt Lemmon Hwy, 5800'	Walsh, B.	03-Jun-2004	BCSC	CS_3264	x	-	-
-	-	*Grammia incorrupta*	USA: AZ: Pima Co, mi. 11 Mt Lemmon Hwy, 5800'	Walsh, B.	03-Jun-2004	BCSC	CS_3265	x	-	-
-	-	*Grammia incorrupta*	USA: AZ: Pima Co, mi. 11 Mt Lemmon Hwy, 5800'	Walsh, B.	03-Jun-2004	BCSC	CS_3266	x	-	-
-	-	*Grammia incorrupta*	USA: AZ: Cochise Co., Huachuca Mtns, Ramsey Cyn Rd	Sternitzky, R.F.	13-Aug-1966	CNC	CS_3337	x	-	-

Appendix 2-1 (cont'd.). Data for morphology and molecular sequence voucher specimens.

cox1 'barcode' haplotype	Clade	Identification	Locality	Collector	Date	Voucher Depostion*	Specimen/ Sample ID	Dissection voucher	GenBank Accession No. **	No. bp *cox1*
-	-	*Grammia incorrupta*	USA: AZ: Pima Co., Tucson		21-Aug-1937	CNC	CS_3234	x	-	-
-	-	*Grammia incorrupta*	USA: KS: Finney Co., Garden City, 13 mi. SE 2800'	Lafontaine & Bowen	25-Aug-1975	CNC	CS_3025	x	-	-
-	-	*Grammia incorrupta*	USA: KS: Seward Co., Liberal, 13 mi NE 2700'	lafontaine & Bowen	26-Jul-1975	CNC	CS_3026	x	-	-
IN1	incorrupta	*Grammia incorrupta*	USA: AZ: Pima Co., Santa Catalina Mtns.	Walsh, B.	03-Jun-2004	BCSC	BCSC253	-	EU119454	658
IN2	incorrupta	*Grammia incorrupta*	USA: NM: Grant Co., Gila R. WA	Ferris, C.	30-Sep-2003	BCSC	BCSC254	-	EU119456	1357
IN3	incorrupta	*Grammia incorrupta*	USA: CO: Mesa Co., Colorado NM	Moore, J.	26-Sep-1999	BCSC	BCSC256	-	EU119455	658
IN4	incorrupta	*Grammia incorrupta*	USA: TX: Hemphill Co., Gene Howe WMA	Segebarth, I.	31-Jul-2005	BIO	06-SUSA-0039	-	n/a	658
-	-	*Grammia kodara*	Russian Federation: Baikal: North Baikal, Kodar village		14-Jul-1999	USNM	CS3007	x	-	-
KO1	kodara	*Grammia kodara*	RUS: Baikal: North Baikal, Kodar	-	14-Jul-1999	USNM	BCSC346	-	EU119458	658
KO2	kodara	*Grammia kodara*	RUS: Baikal: North Baikal, Kodar	-	14-Jul-1999	USNM	BCSC347	-	EU119457	535
-	-	*Grammia margo*	CAN: AB: Opal Sand Hills, 3 km NW of Opal	J.H. Acorn	10-Jun-1984	personal collr	CS3166	x	-	-
-	-	*Grammia margo*	CAN: AB: Fairview, 10 mi. SE	Pike, E. M.	04-May-1961	UASM	CS3167	x	-	-
EA20	eastern	*Grammia margo*	CAN: AB: Edgerton, 7.5km SE	Schmidt, B. C.	01-Jun-2004	UASM	BCSC270	-	EU119507	1357
EA20	eastern	*Grammia margo*	CAN: BC: Peace River	Shepard, J.	07-Jun-1997	RBCM	BCSC250	-	EU119506	590
EA20	eastern	*Grammia margo*	CAN: BC: Peace River	Shepard, J.	24-May-1997	RBCM	BCSC310	-	EU119505	658
EA3	eastern	*Grammia margo*	CAN: AB: Edgerton, 7.5km SE	Anweiler, G. G.	01-Jun-2002	UASM	BCSC269	-	EU119508	658
-	-	*Grammia nevadensis*	USA: UT: Utah Co., Provo, BYU campus	Ferguson, M.	20-Aug-2005	BCSC	BCSC284	x	-	-
-	-	*Grammia nevadensis*	CAN: AB: Kootenay Plains Eco. Res., Whirlpool Pt.	Schmidt, C; Dombroskie, J.	26-Jul-2006	UASM	CS_3280	x	-	-
-	-	*Grammia nevadensis*	CAN: AB: Kootenay Plains Eco. Res., Whirlpool Pt.	Schmidt, C; Dombroskie, J.	26-Jul-2006	UASM	CS_3281	x	-	-
-	-	*Grammia nevadensis*	CAN: AB: Kootenay Plains Eco. Res., Whirlpool Pt.	Schmidt, C; Dombroskie, J.	26-Jul-2006	UASM	CS_3283	x	-	-
-	-	*Grammia nevadensis*	CAN: AB: Kootenay Plains Eco. Res., Whirlpool Pt.	Schmidt, C; Dombroskie, J.	26-Jul-2006	UASM	CS_3284	x	-	-
-	-	*Grammia nevadensis*	CAN: AB: Kootenay Plains Eco. Res., Whirlpool Pt.	Schmidt, C; Dombroskie, J.	26-Jul-2006	UASM	CS_3285	x	-	-

Appendix 2-1 (cont'd.). Data for morphology and molecular sequence voucher specimens.

cox1 'barcode' haplotype	Clade	Identification	Locality	Collector	Date	Voucher Depostion*	Specimen/ Sample ID	Dissection voucher	GenBank Accession No. **	No. bp *cox1*
-	-	*Grammia nevadensis*	CAN: BC: Kanaka Bar	Ife, S; Vandermoor, R.	2005	BCSC	CS_3336	x	-	-
-	-	*Grammia nevadensis*	CAN: BC: Princeton	Reichel,J.	1984	BCSC	CS_3233	x	-	-
-	-	*Grammia nevadensis*	CAN: SK: Burstall	Anweiler, G.; Troubridge, J.	13-Aug-2001	UASM	CS_3258	x	-	-
-	-	*Grammia nevadensis*	CAN: SK: Burstall	Anweiler, G.; Troubridge, J.	13-Aug-2001	UASM	CS_3259	x	-	-
-	-	*Grammia nevadensis*	CAN: SK: Burstall	Anweiler, G.; Troubridge, J.	13-Aug-2001	UASM	CS_3260	x	-	-
-	-	*Grammia nevadensis*	CAN: SK: Burstall	Anweiler, G.; Troubridge, J.	13-Aug-2001	UASM	CS_3261	x	-	-
-	-	*Grammia nevadensis*	CAN: SK: Burstall	Anweiler, G.; Troubridge, J.	13-Aug-2001	UASM	CS_3262	x	-	-
-	-	*Grammia nevadensis*	CAN: SK: Burstall	Anweiler, G.; Troubridge, J.	13-Aug-2001	UASM	CS_3263	x	-	-
-	-	*Grammia nevadensis*	USA: MT: Gates of the Mountains 46 49N 111 59W	Troubridge, J.	11-Sep-1999	BCSC	CS_3023	x	-	-
-	-	*Grammia nevadensis*	USA: WA: Wanapum Dam, 2mi NW	Troubridge, J	17-Sep-1994	BCSC	CS_3020	x	-	-
-	-	*Grammia nevadensis*	CAN: BC: Oliver			CNC	ARCT1078	x	-	-
-	-	*Grammia nevadensis*	CAN: MB: Rounthwaite	Marmont, L.E.	1905	CNC	CS_3236	x	-	-
-	-	*Grammia nevadensis*	CAN: YT: 10 km s. Moose Crk, Klondike Hwy [sage slope]	C. Dondale	04-Jul-1981	CNC	CS_3338	x	-	-
-	-	*Grammia nevadensis*	CAN: YT: Richardson Mtns., 67 58' N 136 29'W	Polak, M; Wood, M.	30-Jun-1987	CNC	CS_3339	x	-	-
BE1	western	*Grammia nevadensis*	USA: WA: Vantage	Troubridge, J. T.	17-Sep-1993	CNC	CNCNoctuoidea 10183	-	EU119617	658
NV1	western	*Grammia nevadensis*	CAN: BC: Kirby Flats	Troubridge, J. T.	20-Aug-1998	CNC	CNCNoctuoidea 10167	-	EU119625	573
NV1	western	*Grammia nevadensis*	CAN: BC: Mount Kobau	Troubridge, J. T.	20-Aug-1999	CNC	CNCNoctuoidea 10186	-	EU119619	570
NV1	western	*Grammia nevadensis*	CAN: BC: Kirby Flats	Troubridge, J. T.	23-Aug-2000	BCSC	BCSC241	-	EU119460	568
NV10	western	*Grammia nevadensis*	USA: CO: Hinsdale Co., Henson Ck. 9350'	Ellingson et al.	08-Jul-1995	CSU	BCSC287	-	EU119463	602
NV11	western	*Grammia nevadensis*	CAN: AB: nr. Empress, Sandy Point cmpgd.	Anweiler, G. G.	13-Aug-2001	UASM	BCSC243	-	EU119466	658
NV12	western	*Grammia nevadensis*	CAN: BC: McGillivray Ck.	Troubridge, J. T.	11-Aug-2000	BCSC	BCSC240	-	EU119459	658

Appendix 2-1 (cont'd.). Data for morphology and molecular sequence voucher specimens.

cox1 'barcode' haplotype	Clade	Identification	Locality	Collector	Date	Voucher Depostion*	Specimen/ Sample ID	Dissection voucher	GenBank Accession No. **	No. bp *cox1*
NV2	western	*Grammia nevadensis*	CAN: AB: Jasper Lake	Troubridge, J. T.	29-Jun-1994	CNC	CNCNoctuoidea 10166	-	EU119624	532
NV2	western	*Grammia nevadensis*	CAN: SK: Burstall	Troubridge, J. T.	13-Aug-2001	CNC	CNCNoctuoidea 10187	-	EU119620	658
NV3	western	*Grammia nevadensis*	CAN: SK: Burstall	Troubridge, J. T.	13-Aug-2001	CNC	CNCNoctuoidea 10188	-	EU119621	658
NV4	western	*Grammia nevadensis*	CAN: BC: Riske Creek	Fischer, A. I.	14-Aug-1996	BIO	CGWC-1131	-	n/a	658
NV5	western	*Grammia nevadensis*	CAN: AB: Writing-on-Stone PP	Anweiler, G. G.	01-Sep-2002	UASM	BCSC242	-	EU119465	658
NV5	western	*Grammia nevadensis*	CAN: BC: Riske Creek	Fischer, A. I.	13-Aug-1996	BIO	CGWC-1130	-	n/a	658
NV5	western	*Grammia nevadensis*	CAN: BC: Riske Creek	Fischer, A. I.	14-Aug-1996	BIO	CGWC-1132	-	n/a	658
NV5	western	*Grammia nevadensis*	CAN: BC: Riske Creek	Fischer, A. I.	12-Aug-1996	BIO	CGWC-1133	-	n/a	658
NV5	western	*Grammia nevadensis*	CAN: BC: Maple Bay	Troubridge, J. T.	13-Aug-1994	CNC	CNCNoctuoidea 10165	-	EU119623	569
NV5	western	*Grammia nevadensis*	CAN: BC: 4 km N invermere	Troubridge, J. T.	16-Aug-1996	CNC	CNCNoctuoidea 10168	-	EU119626	509
NV6	western	*Grammia nevadensis*	CAN: AB: Mt Baldy	Troubridge, J. T.	26-Jul-1998	CNC	CNCNoctuoidea 10164	-	EU119622	611
NV7	western	*Grammia nevadensis*	USA: OR: Catlow Rim	Troubridge, J. T.	05-Sep-1999	CNC	CNCNoctuoidea 10184	-	EU119618	658
NV8	western	*Grammia nevadensis*	USA: UT: Provo	Ferguson, M.	20-Aug-2005	UASM	BCSC284	-	EU119461	658
NV9	western	*Grammia nevadensis*	USA: CO: Hinsdale Co., Henson Ck. 9350'	Ellingson et al.	07-Jul-1995	CSU	BCSC285	-	EU119462	601
NV9	western	*Grammia nevadensis*	USA: CO: Hinsdale Co., Henson Ck. 9350'	Ellingson et al.	08-Jul-1995	CSU	BCSC286	-	EU119464	595
-	-	*Grammia ornata*	CAN: BC: Riondel, 2km S	Schmidt, B. C.		BCSC	CS3184	x	-	-
-	-	*Grammia ornata*	USA: MT: Lewis & Clark Co., Holter L.	Harp, C.	04-Jun-1996	BCSC	CS_3018	x	-	-
-	-	*Grammia ornata*	CAN: BC: Osoyoos	Martin, J.E.H.	14-May-1953	CNC	CS3185	x	-	-
-	-	*Grammia ornata*	USA: OR: Lincoln Co., Newport	J. Troubridge	29-Jul-1995	UASM	CS3183	x	-	-
CP1	western	*Grammia ornata*	CAN: BC: Summerland	Troubridge, J. T.	01-May-1990	CNC	CNCNoctuoidea 10146	-	EU119631[b]	499
OR1	western	*Grammia ornata*	CAN: BC: Seton Lake, E end	Troubridge, J. T.	03-Jun-1995	CNC	CNCNoctuoidea 10142	-	EU119629	579
OR2	western	*Grammia ornata*	USA: OR: Josephine Co., Eight $ Mtn.	Troubridge, J. T.	15-Jun-1999	CNC	CNCNoctuoidea 10138	-	EU119632	602
OR3	western	*Grammia ornata*	USA: OR: Frissell Point	Troubridge, J. T.	25-Jul-1997	CNC	CNCNoctuoidea 10143	-	EU119630	580

Appendix 2-1 (cont'd.). Data for morphology and molecular sequence voucher specimens.

cox1 'barcode' haplotype	Clade	Identification	Locality	Collector	Date	Voucher Depostion*	Specimen/ Sample ID	Dissection voucher	GenBank Accession No. **	No. bp *cox1*
OR4	western	*Grammia ornata*	USA: OR: Newport	Troubridge, J. T.	23-Jul-1995	CNC	CNCNoctuoidea 10140	-	EU119627	553
OR5	western	*Grammia ornata*	CAN: BC: Bummer's Flats, Ft. Steele	Schmidt, B. C.	15-May-2004	UASM	BCSC234	-	EU119473	1357
OR6	western	*Grammia ornata*	CAN: BC: Riondel, 10km N	Anweiler, G. G.	26-Jun-2003	UASM	BCSC235	-	EU119472	1357
OR7	western	*Grammia ornata*	USA: OR: Josephine Co., Eight $ Mtn.	Troubridge, J. T.	15-Jun-1999	CNC	CNCNoctuoidea 10139	-	EU119633	597
OR8	western	*Grammia ornata*	USA: CA: Squirrel Creek, Plumas Co	Troubridge, J. T.	14-Jun-1999	CNC	CNCNoctuoidea 10141	-	EU119628	591
-	-	*Grammia parthenice*	USA: ND: Devil's Lake, 2.5 mi N 1475'	Lafontaine & Lewis	30-Aug-1972	CNC	CS3168	x	-	-
EA18	eastern	*Grammia parthenice*	CAN: AB: Dunvegan	Sperling, F.	19-Jul-2003	UASM	BCSC348	-	EU119478	658
EA18	eastern	*Grammia parthenice*	CAN: BC: Riske Creek	Fischer, A. I.	14-Aug-1996	BIO	CGWC-1124	-	n/a	658
EA18	eastern	*Grammia parthenice*	CAN: BC: Riske Creek	Fischer, A. I.	10-Aug-1996	BIO	CGWC-1125	-	n/a	658
EA18	eastern	*Grammia parthenice*	CAN: BC: Riske Creek	Fischer, A. I.	11-Aug-1996	BIO	CGWC-1126	-	n/a	658
EA18	eastern	*Grammia parthenice*	CAN: BC: Riske Creek	Fischer, A. I.	10-Aug-1996	BIO	CGWC-1127	-	n/a	658
EA18	eastern	*Grammia parthenice*	CAN: BC: Riske Creek	Fischer, A. I.	14-Aug-1996	BIO	CGWC-1128	-	n/a	658
EA18	eastern	*Grammia parthenice*	CAN: BC: Riske Creek	Fischer, A. I.	17-Aug-1996	BIO	CGWC-1129	-	n/a	658
EA19	eastern	*Grammia parthenice*	CAN: AB: Hailstone Butte	Troubridge, J. T.	25-Jul-1996	CNC	CNCNoctuoidea 10066	-	EU119635	565
EA19	eastern	*Grammia parthenice*	CAN: ON: Stittsville	Troubridge, J. T.	15-Aug-2003	BCSC	BCSC349	-	EU119476	658
EA19	eastern	*Grammia parthenice*	CAN: ON: Stittsville	Troubridge, J. T.	15-Aug-2003	CNC	CNCNoctuoidea 10064	-	EU119634	607
EA19	eastern	*Grammia parthenice*	CAN: QC: St-Michel des Saints	Handfield, D.	08-Aug-2005	DHC	DH010702	-	EU119636	658
EA3	eastern	*Grammia parthenice*	CAN: AB: Tolman Bridge	Schmidt, B. C.	18-Jul-2001	BCSC	BCSC293	-	EU119477	658
PA1	parthenice	*Grammia parthenice*	CAN: QC: St-Michel des Saints	Handfield, D.	08-Aug-2005	DHC	DH010703	-	EU119637	658
PA1	parthenice	*Grammia parthenice*	USA: KY: Livingston Co., Riley property	Segebarth, C.	10-Sep-2004	BIO	06-SUSA-0022	-	n/a	658
PA1	parthenice	*Grammia parthenice*	USA: NC	Sullivan, J. B.	?	BIO	05-NCCC-428	-	EU119640	658
PA2	parthenice	*Grammia parthenice*	USA: NC: Alleghany Co., New River SP	Sullivan, J. B.	04-Sep-2002	BIO	06-NCNW-0032	-	EU119639	658
PA3	parthenice	*Grammia parthenice*	USA: NC	Sullivan, J. B.	?	BIO	05-NCCC-429	-	EU119641	617
PA4	parthenice	*Grammia parthenice*	USA: NC: Alleghany Co., New River SP	Sullivan, J. B.	04-Sep-2002	BIO	06-NCNW-0014	-	EU119638	658
PA5	parthenice	*Grammia parthenice*	USA: GA: Whitfield Co., Rocky Face	Adams, J. K.	02-Oct-1993	BCSC	BCSC350	-	EU119475	570

Appendix 2-1 (cont'd.). Data for morphology and molecular sequence voucher specimens.

cox1 'barcode' haplotype	Clade	Identification	Locality	Collector	Date	Voucher Depostion*	Specimen/ Sample ID	Dissection voucher	GenBank Accession No. **	No. bp *cox1*
PA6	parthenica	*Grammia parthenica*	USA: GA: Fairmont, 5mi SE, Bartow Co	Slotten, J.	22-Sep-2001	BCSC	BCSC406	-	EU119474	563
-	-	*Grammia phyllira*	CAN: AB: Wainwright Dunes Ecol. Res.	C.Schmidt	31-Jul-2000	BCSC	CS3158	x	-	-
-	-	*Grammia phyllira*	CAN: AB: Wainwright Dunes Ecol. Res.	C.Schmidt	31-Jul-2000	BCSC	CS3177	x	-	-
-	-	*Grammia phyllira*	USA: MO: Wayne Co., Williamsville	Becker, EC	07-Jul-1955	CNC	CS3176	x	-	-
PY1	phyllira	*Grammia phyllira*	CAN: AB: Slegner Lake sandhills	Schmidt, B. C.	25-Jul-2004	UASM	BCSC266	-	EU119482	1357
PY2	phyllira	*Grammia phyllira*	CAN: AB: Slegner Lake sandhills	Schmidt, B. C.	25-Jul-2004	UASM	BCSC267	-	EU119483	658
PY3	phyllira	*Grammia phyllira*	USA: KY: McCracken Co., Reidland	Segebarth, I.	31-May-2006	BIO	06-SUSA-0123	-	n/a	656
PY4	phyllira	*Grammia phyllira*	USA: KY: Metcalfe Co., N of Center	Cook, C.	?	BCSC	BCSC307	-	EU119484	601
PY5	phyllira	*Grammia phyllira*	CAN: ON: Ottawa, Jinkinson Rd.	Troubridge, J. T.	15-Jul-2003	BCSC	BCSC265	-	EU119479	1357
PY6	phyllira	*Grammia phyllira*	CAN: ON: Ottawa, Jinkinson Rd.	Troubridge, J. T.	15-Jul-2003	BCSC	BCSC264	-	EU119480	1357
PY6	phyllira	*Grammia phyllira*	CAN: ON: Stittsville	Troubridge, J. T.	30-Jul-2004	CNC	CNCNoctuoidea 10137	-	EU119642	658
PY7	phyllira	*Grammia phyllira*	USA: CO: Jefferson Co., Lookout Mtn.	Bowman, D.	13-Jul-1996	CNC	BCSC263	-	EU119485	658
-	-	*Grammia placentia*	USA: NJ: Lakehurst	Lemmer, F.	11 July	CNC	CS3173	x	-	-
-	-	*Grammia placentia*	USA: NJ: Lakehurst	Lemmer, F.	21 June	CNC	CS3174	x	-	-
PL1	placentia	*Grammia placentia*	USA: FL: Ocala Nat For, Putnam Co	Slotten, J.	11-Oct-2001	BCSC	BCSC298	-	n/a	1357
PL1	placentia	*Grammia placentia*	USA: GA: Emamuel Co., Ohoopee Dunes	Adams, J. K.	12-Oct-2003	BIO	06-JKA-0019	-	n/a	596
PL2	placentia	*Grammia placentia*	USA: GA: Emamuel Co., Ohoopee Dunes	Adams, J. K.	12-Oct-2003	BIO	06-JKA-0020	-	n/a	593
PL2	placentia	*Grammia placentia*	USA: GA: Long Co., Ludowici	Adams, J. K. & E.	13-May-2004	BCSC	BCSC276	-	EU119488	658
PL3	placentia	*Grammia placentia*	USA: GA: Emamuel Co., Ohoopee Dunes	Adams, J. K.	12-Oct-2003	BIO	06-JKA-0018	-	n/a	603
PL4	placentia	*Grammia placentia*	USA: GA: 8 mi. W Swainsboro	Adams, J. K. et al.	10-May-2004	BCSC	BCSC277	-	EU119487	658
-	-	*Grammia quenseli*	CAN; NU: Pelly Bay			CNC	ARCT1062	x	-	-

Appendix 2-1 (cont'd.). Data for morphology and molecular sequence voucher specimens.

cox1 'barcode' haplotype	Clade	Identification	Locality	Collector	Date	Voucher Depostion*	Specimen/ Sample ID	Dissection voucher	GenBank Accession No. **	No. bp *cox1*
-	-	*Grammia quenseli*	CAN: BC: Pink Mtn.	Pike, E.M.	08-Jul-1978	UASM	CS_3004	x	-	-
EA11	eastern	*Grammia quenseli*	CAN: BC: Summit L., 2km N	Troubridge, J. T.	19-Jun-1990	CNC	BCSC340	-	EU119499	585
EA11	eastern	*Grammia quenseli*	CAN: MB: Churchill, 24km NE	Hensel, H.	22-Jul-2002	CNC	BCSC343	-	EU119495	658
EA11	eastern	*Grammia quenseli*	CAN: MB: Churchill, 24km NE	Hensel, H.	11-Jul-2001	CNC	BCSC344	-	EU119493	658
EA31	eastern	*Grammia quenseli*	CAN: BC: Pink Mtn.	Schmidt, B. C.	16-Jul-1992	BCSC	BCSC339	-	EU119489	658
EA32	eastern	*Grammia quenseli*	CAN: MB: Churchill, 24km NE	Hensel, H.	11-Jul-2001	CNC	BCSC342	-	EU119491	658
QE1	kodara	*Grammia quenseli*	CAN: MB: Churchill, 24km NE	Hensel, H.	18-Jul-2001	CNC	BCSC345	-	EU119496	658
QE3	western	*Grammia quenseli*	CAN: YT: Ogilvie Mtns., Mt. Bouvette	Lafontaine, D.	05-Jul-1985	CNC	BCSC336	-	EU119490	599
YK1	western	*Grammia quenseli*	CAN: YT: Dempster Hwy km 67	Beck, B. & J.	24-Jun-2005	BCSC	BCSC418	-	EU119492	585
-	-	*Grammia ursina*	USA: CA: Riverside Co., Gavilan Hills	Sala, F.	11-Jul-1986	BERK	CS_3340	x	-	-
-	-	*Grammia ursina*	USA: CA: Orange Co., Dana Point		29-Sep-1936	CNC	CS_3232	x	-	-
-	-	*Grammia ursina*	USA: CA: Orange Co., Dana Point		02-Oct-1936	CNC	CS_3342	x	-	-
-	-	*Grammia ursina*	USA: CA: Riverside Co., Gavilan Hills	McBurney, J.T.	06-Aug-1989	LACM	CS3159	x	-	-
UR1	ursina	*Grammia ursina*	USA: CA: LA Co., San Clemente Is.	Powell, J.; Benedictis, J.	27-Sep-2002	UCB	BCSC256	-	EU119501	658
UR2	ursina	*Grammia ursina*	USA: CA: LA Co., San Clemente Is.	Powell, J.; Benedictis, J.	27-Sep-2002	UCB	BCSC257	-	EU119503	658
-	-	*Grammia virgo*	CAN: AB: Peace River, 6 km NNE		04-Jul-2003	BCSC	CS3017	x	-	-
-	-	*Grammia virgo*	CAN: NS: Kings Co., Kentville		29-Jul-1989	BCSC	CS3172	x	-	-
-	-	*Grammia virgo*	USA: NC: Highlands	Durden, C.J.	26-Jul-1957	CNC	CS_3034	x	-	-
-	-	*Grammia virgo*	CAN: AB: Rumsey Ecol. Res., nr. Big Valley	BCS	26-Jun-1998	BCSC	CS3170	x	-	-
VI1	virgo	*Grammia virgo*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	11-Jul-2004	BIO	04HBL005105	-	n/a	658
VI1	virgo	*Grammia virgo*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	15-Jul-2004	BIO	04HBL005184	-	n/a	658
VI1	virgo	*Grammia virgo*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	15-Aug-2005	BIO	2005-ONT-1480	-	n/a	658
VI1	virgo	*Grammia virgo*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	?	BIO	APAN2.01	-	AF549821	617
VI1	virgo	*Grammia virgo*	USA: PA: 6 mi S Sunbury	Adams, J. K.	11-Jul-2004	BCSC	BCSC353	-	EU119512	658

Appendix 2-1 (cont'd.). Data for morphology and molecular sequence voucher specimens.

cox1 'barcode' haplotype	Clade	Identification	Locality	Collector	Date	Voucher Depostion*	Specimen/ Sample ID	Dissection voucher	GenBank Accession No. **	No. bp *cox1*
VI1	virgo	*Grammia virgo*	CAN: QC: Val-des-Monts, Lac Barnes	Handfield, D.	18-Jul-2005	DHC	DH010609	-	EU119644	658
VI10	virgo	*Grammia virgo*	CAN: NB: Charlotte Co., St. Andrews	Hebert, P. D. N.	18-Jul-2002	BIO	04HBL007604	-	n/a	658
VI11	virgo	*Grammia virgo*	CAN: AB: Johnson Creek	Troubridge, J. T.	16-Aug-2001	CNC	CNCNoctuoidea 10065	-	EU119643	599
VI12	virgo	*Grammia virgo*	USA: NC	Sullivan, J. B.	?	BIO	05-NCCC-426	-	EU119645	658
VI13	virgo	*Grammia virgo*	USA: NC: Swain Co.	Segebarth, K.	20-Jul-2004	BIO	DNA-ATBI-0624	-	n/a	609
VI13	virgo	*Grammia virgo*	USA: NC: Swain Co.	Segebarth, K.	20-Jul-2004	BIO	DNA-ATBI-1142	-	n/a	548
VI13	virgo	*Grammia virgo*	USA: NC: Swain Co.	Segebarth, K.	20-Jul-2004	BIO	DNA-ATBI-1143	-	n/a	653
VI13	virgo	*Grammia virgo*	USA: TN: Great Smoky Mountains NP	Goldstein, P.	25-Jul-2000	UCB	BCSC354	-	EU119610	658
VI13	virgo	*Grammia virgo*	USA: TN: Sevier Co., Gatlinburg	Hebert, P. D. N.	20-Jul-2004	BIO	04HBL002148	-	n/a	609
VI14	kodara	*Grammia virgo*	USA: NC	Sullivan, J. B.	?	BIO	05-NCCC-427	-	EU119646	658
VI15	western	*Grammia virgo*	USA: GA: Bartow Co.	Adams, J. K.	17-Sep-2005	BIO	06-JKA-0003	-	n/a	658
VI2	virgo	*Grammia virgo*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	11-Jul-2004	BIO	04HBL005060	-	n/a	658
VI4	virgo	*Grammia virgo*	CAN: NB: Charlotte Co., St. Andrews	Ballantyne, J.	09-Aug-2005	BIO	05-NBSTA-560	-	n/a	658
VI5	virgo	*Grammia virgo*	CAN: NB: Charlotte Co., St. Andrews	Hebert, P. D. N.	15-Jul-2003	BIO	Moth 407.03SA	-	n/a	658
VI6	virgo	*Grammia virgo*	CAN: ON: Stittsville	Troubridge, J. T.	10-Jul-2003	BCSC	BCSC352	-	EU119613	658
VI7	virgo	*Grammia virgo*	CAN: NB: Charlotte Co., St. Andrews	Ballantyne, J.	28-Jul-2005	BIO	05-NBSTA-050	-	n/a	658
VI7	virgo	*Grammia virgo*	CAN: NB: Sunbury Co., Acadia Res. Forest	Thomas, A. W.	22-Jul-2002	BIO	MNBTT-972	-	n/a	658
VI7	virgo	*Grammia virgo*	CAN: NB: Charlotte Co., St. Andrews	Hebert, P. D. N.	20-Jul-2002	BIO	moth217.02SA	-	n/a	639
VI8	virgo	*Grammia virgo*	CAN: AB: Edgerton, 7.5km SE	Schmidt, B. C.	15-Jul-2003	UASM	BCSC291	-	EU119611	1357
VI9	virgo	*Grammia virgo*	CAN: NB: Sunbury Co., Acadia Res. Forest	Thomas; A. W.	17-Jul-2002	BIO	MNBTT-971	-	n/a	658
-	-	*Grammia virguncula*	CAN: NF: St. Anthony			CNC	ARCT1060	x	-	-
-	-	*Grammia virguncula*	CAN: AB: Wagner Natural Area	Lawrie, D.	11-Jul-1998	UASM	CS_3000	x	-	-
-	-	*Grammia virguncula*	CAN: AB: Wainwright Dunes	Anweiler, G. G.	13-Jul-2002	UASM	CS_3008	x	-	-
EA1	eastern	*Grammia virguncula*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	09-Jun-2004	BIO	04HBL005274	-	n/a	658

Appendix 2-1 (cont'd.). Data for morphology and molecular sequence voucher specimens.

cox1 'barcode' haplotype	Clade	Identification	Locality	Collector	Date	Voucher Deposition*	Specimen/ Sample ID	Dissection voucher	GenBank Accession No. **	No. bp *cox1*
EA1	eastern	*Grammia virguncula*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	17-Jun-2004	BIO	04HBL005552	-	n/a	658
EA1	eastern	*Grammia virguncula*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	19-Jun-2004	BIO	04HBL005586	-	n/a	606
EA1	eastern	*Grammia virguncula*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	07-Jun-2006	BIO	2006-ONT-0686	-	n/a	658
EA1	eastern	*Grammia virguncula*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	08-Jun-2006	BIO	2006-ONT-0721	-	n/a	658
EA10	eastern	*Grammia virguncula*	CAN: QC: Saint-Narcisse	Handfield, D.	23-Jun-2005	DHC	DH010683	-	EU119659	617
EA11	eastern	*Grammia virguncula*	CAN: AB: Birch Mtns., Gardiner L.	Hilchie, G.	09-Jul-2004	UASM	BCSC333	-	EU119635	1357
EA12	eastern	*Grammia virguncula*	CAN: AB: Birch Mtns., Sand R.	Hilchie, G.	09-Jul-2004	UASM	BCSC334	-	EU119633	658
EA13	eastern	*Grammia virguncula*	CAN: QC: Laverendrye Pk.	Troubridge, J. T.	30-Jun-2003	CNC	BCSC335	-	EU119534	1357
EA14	eastern	*Grammia virguncula*	CAN: NS: Guysborough Co.	Bridgehouse, D.	23-Jul-1996	BCSC	BCSC328	-	EU119516	658
EA14	eastern	*Grammia virguncula*	CAN: NS: Mt. Uniacke, Hants Co.	Bridgehouse, D.	20-Jul-1999	BCSC	BCSC294	-	EU119622	658
EA14	eastern	*Grammia virguncula*	CAN: NS: Mt. Uniacke, Hants Co.	Bridgehouse, D.	20-Jul-1999	BCSC	BCSC295	-	EU119521	658
EA14	eastern	*Grammia virguncula*	CAN: NS: Shelburne Co., Cape Sable	-	22-Jul-1986	BCSC	BCSC322	-	EU119629	596
EA15	eastern	*Grammia virguncula*	USA: WI: Fond du Lac Co., Little Mud L.	Holbach, G.	12-Jun-1988	BCSC	BCSC312	-	EU119520	521
EA16	eastern	*Grammia virguncula*	USA: WY: Albany Co, Gelatt Lake	Ferris, C.	29-Jul-2002	CNC	BCSC318	-	EU119519	1357
EA17	eastern	*Grammia virguncula*	CAN: AB: Calling L., 11km S	Schmidt, B. C.	07-Jul-2001	BCSC	BCSC319	-	EU119517	658
EA18	eastern	*Grammia virguncula*	CAN: ON: Carp	Troubridge, J. T.	28-Jun-2003	BCSC	BCSC320	-	EU119627	1357
EA19	eastern	*Grammia virguncula*	CAN: SK: Crooked L., Melville beach	Anweiler, G. G.	10-Jul-1997	UASM	BCSC321	-	EU119524	658
EA2	eastern	*Grammia virguncula*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	07-Jun-2006	BIO	2006-ONT-0665	-	n/a	658
EA20	eastern	*Grammia virguncula*	CAN: AB: Junction Mtn.	Pike, E. M.	26-Aug-2000	UASM	BCSC325	-	EU119532	658
EA20	eastern	*Grammia virguncula*	CAN: AB: Water Valley, 16mi W	Lawrie, D.	14-Jul-1990	UASM	BCSC327	-	EU119518	658
EA20	eastern	*Grammia virguncula*	CAN: YT: St. Elias Rge., Mt. Archibald	Troubridge, J. T.	23-Jun-1991	CNC	BCSC324	-	EU119528	571
EA21	eastern	*Grammia virguncula*	CAN: AB: Sundre, Nitchi Ck.	Schmidt, B. C.	24-Jun-1990	BCSC	BCSC331	-	EU119515	572
EA22	eastern	*Grammia virguncula*	CAN: AB: Opal	Troubridge, J. T.	12-Jul-1999	CNC	CNCNoctuoidea 10161	-	EU119648	658

Appendix 2-1 (cont'd.). Data for morphology and molecular sequence voucher specimens.

cox1 'barcode' haplotype	Clade	Identification	Locality	Collector	Date	Voucher Depostion*	Specimen/ Sample ID	Dissection voucher	GenBank Accession No. **	No. bp *cox1*
EA3	eastern	*Grammia virguncula*	CAN: ON: Carp	Troubridge, J. T.	25-Jun-2004	CNC	CNCNoctuoidea 10163	-	EU119650	658
EA3	eastern	*Grammia virguncula*	CAN: ON: Ottawa, Jinkinson Rd	Troubridge, J. T.	03-Jul-2003	CNC	CNCNoctuoidea 10162	-	EU119649	658
EA3	eastern	*Grammia virguncula*	CAN: ON: Pakenham alvar	Troubridge, J. T.	01-Aug-2005	CNC	CNCNoctuoidea 12105	-	EU119660	658
EA3	eastern	*Grammia virguncula*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	17-Jun-2004	BIO	04HBL005553	-	n/a	658
EA3	eastern	*Grammia virguncula*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	19-Jun-2004	BIO	04HBL005585	-	n/a	658
EA3	eastern	*Grammia virguncula*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	08-Jun-2005	BIO	2005-ONT-168	-	n/a	658
EA3	eastern	*Grammia virguncula*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	13-Jun-2005	BIO	2005-ONT-233	-	n/a	658
EA3	eastern	*Grammia virguncula*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	15-Apr-2003	BIO	Moth4346.03	-	n/a	658
EA3	eastern	*Grammia virguncula*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	15-Apr-2003	BIO	Moth4476.03	-	n/a	574
EA3	eastern	*Grammia virguncula*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	16-Jun-2001	BIO	moth632[illegible]	-	n/a	639
EA3	eastern	*Grammia virguncula*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	?	BIO	moth691.01	-	AF549620	617
EA3	eastern	*Grammia virguncula*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	21-Jun-2001	BIO	moth796.01	-	n/a	639
EA3	eastern	*Grammia virguncula*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	18-Jun-2005	BIO	2005-ONT-386	-	n/a	505
EA3	eastern	*Grammia virguncula*	USA: PA: Tioga Co., 3.5mi NE Liberty	Johnson, S.	23-Jun-2001	BCSC	BCSC323	-	EU119525	658
EA3	eastern	*Grammia virguncula*	USA: VT: Ferdinand	Grehan, J.	20-Jun-1995	USNM	BCSC329	-	EU119523	563
EA4	eastern	*Grammia virguncula*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	15-Jun-2005	BIO	2005-ONT-120	-	n/a	658
EA5	eastern	*Grammia virguncula*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	16-Jun-2005	BIO	2005-ONT-443	-	n/a	658
EA6	eastern	*Grammia virguncula*	CAN: NB: Sunbury Co., Acadia Res. Forest	Thomas, A. W.	27-Jun-2000	BIO	MNBTT-970	-	n/a	658
EA7	eastern	*Grammia virguncula*	CAN: NB: Sunbury Co., Acadia Res. Forest	Thomas, A. W.	08-Jun-2000	BIO	MNBTT-027	-	n/a	658
EA7	eastern	*Grammia virguncula*	CAN: ON: Wellington Co., Puslinch Twp.	Hebert, P. D. N.	19-Jun-2005	BIO	2005-ONT-375	-	n/a	658

Appendix 2-1 (cont'd.). Data for morphology and molecular sequence voucher specimens.

cox1 'barcode' haplotype	Clade	Identification	Locality	Collector	Date	Voucher Depostion*	Specimen/ Sample ID	Dissection voucher	GenBank Accession No. **	No. bp *cox1*
EA7	eastern	*Grammia virguncula*	CAN: QC: Pontiac, Chutes de Luskville	Handfield, D.	10-Jun-2005	DHC	DH010802	-	EU119657	584
EA7	eastern	*Grammia virguncula*	CAN: QC: Pontiac, Chutes de Luskville	Handfield, D.	10-Jun-2005	DHC	DH010803	-	EU119658	658
EA7	eastern	*Grammia virguncula*	CAN: QC: Saint-Narcice	Handfield, D.	05-Aug-2005	DHC	DH010905	-	EU119656	617
EA7	eastern	*Grammia virguncula*	USA: VT: Ferdinand	Griggs, M. S.	30-Jun-1995	USNM	BCSC330	-	EU119526	658
EA8	eastern	*Grammia virguncula*	CAN: NS: Sheffield Mills, Kings Co.	Bridgehouse, D.	22-Jul-2004	BCSC	BCSC296	-	EU119530	658
EA8	eastern	*Grammia virguncula*	CAN: QC: St-Michel des Saints	Handfield, D.	29-Jun-2005	DHC	DH010294	-	EU119655	658
EA8	eastern	*Grammia virguncula*	USA: WI: Sheboygan Co., 3 mi W Widdell	Holbach, G.	12-Jun-1988	BCSC	BCSC311	-	EU119531	515
EA9	eastern	*Grammia virguncula*	CAN: NB: Sunbury Co., Acadia Res. Forest	Thomas, A. W.	27-Jun-2000	BIO	MNBTT-969	-	n/a	658
VR1	western	*Grammia virguncula*	CAN: QC: 10 km SE Degelis	Hensel, H.	16-Jun-1996	CNC	CNCNoctuoidea 10160	-	EU119647	522
-	-	*Grammia williamsii*	CAN: AB: Waterton Lakes NP, Blakiston Ck. fan	Schmidt, B. C.	10-Jul-2005	UASM	CS_3255	x	-	-
-	-	*Grammia williamsii*	CAN: AB: Waterton Lakes NP, Blakiston Ck. fan	Schmidt, B. C.	10-Jul-2005	UASM	CS_3256	x	-	-
-	-	*Grammia williamsii*	CAN: AB: Waterton Lakes NP, Blakiston Ck. fan	Schmidt, B. C.	10-Jul-2005	UASM	CS_3257	x	-	-
-	-	*Grammia williamsii*	CAN: AB: Waterton Lakes NP, Blakiston Ck. fan	Schmidt, B. C.	10-Jul-2005	UASM	CS_3274	x	-	-
-	-	*Grammia williamsii*	CAN: AB: Waterton Lakes NP, Blakiston Ck. fan	Schmidt, B. C.	10-Jul-2005	UASM	CS_3275	x	-	-
-	-	*Grammia williamsii*	USA: NV: Angel Cr. Cmpgd, Elko Co.	Troubridge, J.T.; Lafontaine, D.	22-Jul-2001	BCSC	BCSC249	x	-	-
-	-	*Grammia williamsii*	CAN: SK: Tobin L., 30 km NE Nipawin	Roe, A.	02-Jul-2006	UASM	CS_3267	x	-	-
-	-	*Grammia williamsii*	CAN: SK: Tobin L., 30 km NE Nipawin	Roe, A.	02-Jul-2006	UASM	CS_3268	x	-	-
-	-	*Grammia williamsii*	CAN: SK: Tobin L., 30 km NE Nipawin	Roe, A.	02-Jul-2006	BCSC	CS_3269	x	-	-
-	-	*Grammia williamsii*	CAN: AB: Dunvegan	Schmidt, C.	30-May-2005	UASM	CS_3019	x	-	-
-	-	*Grammia williamsii*	CAN: AB: Jenner, 10km N	Schmidt, B. C.	04-Jun-2004	UASM	CS_3276	x	-	-
-	-	*Grammia williamsii*	CAN: AB: Jenner, 10km N	Schmidt, B. C.	04-Jun-2004	UASM	CS_3277	x	-	-
-	-	*Grammia williamsii*	USA: CO: State Bridge, nr Bonds 7000'	Mackay, MR	23-Jun-1961	CNC	CS_3279	x	-	-

Appendix 2-1 (cont'd.). Data for morphology and molecular sequence voucher specimens.

cox1 'barcode' haplotype	Clade	Identification	Locality	Collector	Date	Voucher Depostion*	Specimen/ Sample ID	Dissection voucher	GenBank Accession No. **	No. bp *cox1*
-	-	*Grammia williamsii*	USA: UT: Beaver Co., Beaver, 5 mi E 6300'	Hardwick, DF	28-Aug-1965	CNC	CS3196	x	-	-
-	-	*Grammia williamsii*	USA: UT: Enterprise, 18mi SE 6800'	Hardwick, DF	31-Aug-1965	CNC	CS3194	x	-	-
-	-	*Grammia williamsii*	USA: UT: Hanksville, 24 mi S Henry Mtns 7500'	Martin, JEH	18-Jul-1968	CNC	CS3195	x	-	-
-	-	*Grammia williamsii*	USA: UT: Mayfield, 6mi E 6500'	Hardwick, DF	25-Aug-1965	CNC	CS3197	x	-	-
-	-	*Grammia williamsii*	USA: WY: Lincoln Co., Smoot, 14 mi S 6900'	Hardwick, DF	22-Aug-1964	CNC	CS_3278	x	-	-
-	-	*Grammia williamsii*	CAN: AB: Drumheller, Midland	Pike, E. M.	10-Jun-1987	UASM	CS_3235	x	-	-
BK1	western	*Grammia williamsii*	CAN: AB: Writing on Stone PP	Troubridge, J. T.	28-Jun-2000	CNC	CNCNoctuoidea 10135	-	EU119664	589
BO1	western	*Grammia williamsii*	USA: WY: Laramie, 7500'	Ferris, C.	01-Jun-2000	BCSC	BCSC363	-	EU119538	658
EA10	eastern	*Grammia williamsii*	CAN: NB: Kouchibouguac NP	Lafontaine, D.	03-Aug-1977	CNC	BCSC380	-	EU119571	491
EA11	eastern	*Grammia williamsii*	CAN: AB: Birch Mtns., Gardiner L.	Macaulay, D. & S.	10-Jul-2004	UASM	BCSC381	-	EU119542	658
EA11	eastern	*Grammia williamsii*	CAN: AB: Redwater Natural Area	Schmidt, B. C.	20-Jul-1999	BCSC	BCSC[illegible]	-	EU119567	658
EA11	eastern	*Grammia williamsii*	CAN: AB: Redwater Natural Area	Schmidt, B. C.	29-Jul-1999	BCSC	BCSC356	-	EU119537	658
EA13	eastern	*Grammia williamsii*	CAN: QC: St-Michel des Saints	Handfield, D.	29-Jun-2005	DHC	DH010293	-	EU119663	658
EA20	eastern	*Grammia williamsii*	CAN: AB: Birch Mtns., Gardiner L.	Macaulay, D. & S.	14-Jul-2004	UASM	BCSC383	-	EU119558	658
EA20	eastern	*Grammia williamsii*	CAN: AB: Opal	Troubridge, J. T.	12-Jul-1999	CNC	CNCNoctuoidea 10136	-	EU119665	572
EA20	eastern	*Grammia williamsii*	CAN: AB: Redwater Natural Area	Schmidt, B. C.	29-Jul-1999	BCSC	BCSC357	-	EU119566	658
EA24	eastern	*Grammia williamsii*	CAN: QC: St-Michel des Saints	Handfield, D.	29-Jun-2005	DHC	DH010291	-	EU119661	658
EA24	eastern	*Grammia williamsii*	CAN: QC: St-Michel des Saints	Handfield, D.	29-Jun-2005	DHC	DH010292	-	EU119662	658
EA25	eastern	*Grammia williamsii*	CAN: AB: Grande Cache, Mt. Stearn	Lawrie, D.	18-Jul-1998	UASM	BCSC367	-	EU119543	658
EA25	eastern	*Grammia williamsii*	CAN: AB: Grande Cache, Mt. Stearn	Lawrie, D.	18-Jul-1998	UASM	BCSC368	-	EU119553	658
EA25	eastern	*Grammia williamsii*	CAN: AB: Jasper NP, Palisades	Schmidt, B. C.	08-Jul-1998	UASM	BCSC369	-	EU119552	658

Appendix 2-1 (cont'd.). Data for morphology and molecular sequence voucher specimens.

cox1 'barcode' haplotype	Clade	Identification	Locality	Collector	Date	Voucher Depostion*	Specimen/ Sample ID	Dissection voucher	GenBank Accession No. **	No. bp *cox1*
EA25	eastern	*Grammia williamsii*	CAN: AB: Jasper NP, Palisades	Schmidt, B. C.	08-Jul-1998	UASM	BCSC370	-	EU119561	658
EA26	eastern	*Grammia williamsii*	CAN: AB: Fidler-Greywillow Wildland Park	Lawrie, D.	18-Jul-2001	UASM	BCSC382	-	EU119541	658
WI1	kodara	*Grammia williamsii*	CAN: AB: Ft. Assiniboine, 6km S	Schmidt, B. C.	02-Aug-1999	UASM	BCSC358	-	EU119539	658
WI10	western	*Grammia williamsii*	CAN: AB: Jenner, 10km N	Schmidt, B. C.	04-Jun-2004	UASM	BCSC388	-	EU119574	658
WI11	western	*Grammia williamsii*	USA: WY: Albany Co.	Ferris, C.	13-Jun-2000	CNC	BCSC364	-	EU119573	658
WI12	western	*Grammia williamsii*	USA: UT: Tooele Co.	Lawrie, D.	17-Jun-2000	BCSC	BCSC301	-	EU119580	658
WI13	western	*Grammia williamsii*	USA: UT: Tooele Co.	Lawrie, D.	17-Jun-2000	BCSC	BCSC302	-	EU119578	658
WI13	western	*Grammia williamsii*	USA: UT: Tooele Co.	Lawrie, D.	17-Jun-2000	BCSC	BCSC303	-	EU119579	658
WI13	western	*Grammia williamsii*	USA: UT: Tooele Co.	Lawrie, D.	17-Jun-2000	BCSC	BCSC304	-	EU119575	658
WI13	western	*Grammia williamsii*	USA: UT: Tooele Co.	Lawrie, D.	17-Jun-2000	BCSC	BCSC305	-	EU119577	519
WI13	western	*Grammia williamsii*	USA: UT: Tooele Co.	Lawrie, D.	17-Jun-2000	BCSC	BCSC306	-	EU119576	658
WI14	western	*Grammia williamsii*	USA: NV: Angel Cr. Cmpgd, Elko Co.	Troubridge, J. T.; Lafontaine, D.	22-Jul-2001	BCSC	BCSC249	-	EU119549	1357
WI14	western	*Grammia williamsii*	USA: NV: Angel L., Elko Co.	Troubridge, J. T.; Lafontaine, D.	23-Jul-2001	BCSC	BCSC359	-	EU119536	658
WI14	western	*Grammia williamsii*	USA: NV: Angel L., Elko Co.	Troubridge, J. T.; Lafontaine, D.	23-Jul-2001	BCSC	BCSC360	-	EU119568	658
WI2	western	*Grammia williamsii*	CAN: AB: Maycroft, W of, Dutch Ck cmpgd.	Roe, A; Lumley, L.	05-Jul-2005	UASM	BCSC372	-	EU119560	658
WI3	western	*Grammia williamsii*	CAN: AB: Jenner, 10km N	Schmidt, B. C.	04-Jun-2004	UASM	BCSC390	-	EU119545	658
WI3	western	*Grammia williamsii*	CAN: AB: Maycroft, W of, Dutch Ck cmpgd.	Roe, A; Lumley, L.	05-Jul-2005	UASM	BCSC374	-	EU119557	658
WI3	western	*Grammia williamsii*	CAN: AB: Maycroft, W of, Dutch Ck cmpgd.	Roe, A; Lumley, L.	05-Jul-2005	UASM	BCSC375	-	EU119544	658
WI4	western	*Grammia williamsii*	USA: WY: Laramie, 7500'	Ferris, C.	05-Jun-2000	BCSC	BCSC362	-	EU119540	658
WI5	western	*Grammia williamsii*	USA: WY: Laramie, 7500'	Ferris, C.	05-Jun-2000	BCSC	BCSC361	-	EU119563	658
WI6	western	*Grammia williamsii*	CAN: BC: Cranbrook	Janz, L.	22-Jun-1992	UASM	BCSC377	-	EU119555	634
WI6	western	*Grammia williamsii*	CAN: BC: Cranbrook	Janz, L.	22-Jun-1992	UASM	BCSC378	-	EU119559	510
WI6	western	*Grammia williamsii*	CAN: BC: Cranbrook	Janz, L.	07-Jul-1996	UASM	BCSC379	-	EU119556	658
WI6	western	*Grammia williamsii*	CAN: BC: Elko, 11km SSW	Schmidt, B. C.	18-May-2004	UASM	BCSC376	-	EU119548	658
WI7	western	*Grammia williamsii*	USA: WY: Albany Co.	Ferris, C.	13-Jun-2000	CNC	BCSC365	-	EU119562	658
WI8	western	*Grammia williamsii*	CAN: AB: Jenner, 10km N	Schmidt, B. C.	04-Jun-2004	UASM	BCSC386	-	EU119547	658
WI8	western	*Grammia williamsii*	CAN: AB: Jenner, 10km N	Schmidt, B. C.	04-Jun-2004	UASM	BCSC387	-	EU119546	658
WI8	western	*Grammia williamsii*	CAN: AB: Jenner, 10km N	Schmidt, B. C.	04-Jun-2004	UASM	BCSC389	-	EU119551	658
WI8	western	*Grammia williamsii*	CAN: AB: Maycroft, W of, Dutch Ck cmpgd.	Roe, A; Lumley, L.	05-Jul-2005	UASM	BCSC373	-	EU119569	658

Appendix 2-1 (cont'd.). Data for morphology and molecular sequence voucher specimens.

cox1 'barcode' haplotype	Clade	Identification	Locality	Collector	Date	Voucher Depostion*	Specimen/ Sample ID	Dissection voucher	GenBank Accession No. **	No. bp *cox1*
WI8	western	*Grammia williamsii*	CAN: AB: Peace River, 8km NNE	Walty, D.	04-Jul-2003	UASM	BCSC26	-	EU119554	658
WI8	western	*Grammia williamsii*	CAN: AB: Peace River, 8kmNNE	Walty, D.	04-Jul-2003	UASM	BCSC25	-	EU119572	658
WI8	western	*Grammia williamsii*	CAN: AB: Peace River, 8kmNNE	Walty, D.	04-Jul-2003	UASM	BCSC27	-	EU119550	658
WI8	western	*Grammia williamsii*	CAN: AB: Waterton Lakes NP.	Schmidt, B. C.	10-Jul-2005	UASM	BCSC371	-	EU119565	658
WI9	western	*Grammia williamsii*	USA: AZ: Apache Co., White Mtns., Greer	Adams, J. K.	28-Jul-2005	BCSC	BCSC366	-	EU119564	658
-	-	*Grammia yavapai*	USA: AZ: Coconino Co., Parks 7100'		26-Jun-1957	LACM	CS3191	x	-	-
YK1	western	*Grammia yukona*	CAN: YT: Kusawa Lake	Schmidt, B. C.	27-Jun-2004	UASM	BCSC259	-	EU119502	1357
YK1	western	*Grammia yukona*	CAN: YT: Kusawa Lake	Schmidt, B. C.	27-Jun-2004	UASM	BCSC260	-	EU119504	1357
-	-	*Holarctia obliterata*	CAN: AB: Little Fish PP, 14 km NE Dorothy	Sperling, F. A. H.	18-Aug-2003	UASM	CS_3013	x	-	-
-	-	*Holarctia obliterata*	CAN: AB: Peace River, 8km NNE (NE21-84-21-W5)	Walty, D.	17-Aug-2003	BCSC	CS_3001	x	-	-
-	-	*Holarctia obliterata*	CAN: AB: Pocahontas	Bowman, K.	31-Jul-1917	UASM	CS_3006	x	-	-
OB1	OUTGROUP	*Holarctia obliterata*	CAN: AB: Dunvegan	Schmidt, B. C.	14-Aug-2003	UASM	BCSC314	-	EU119471	658
OB2	OUTGROUP	*Holarctia obliterata*	CAN: AB: Dunvegan	Schmidt, B. C.	14-Aug-2003	UASM	BCSC315	-	EU119467	658
OB3	OUTGROUP	*Holarctia obliterata*	CAN: AB: Cardinal River Rec Area	Schmidt, B. C.	06-Aug-1989	BCSC	BCSC313	-	EU119468	540
-	OUTGROUP	*Platarctia parthenos*	CAN: AB: Peace River, 8km NW	Hood, B.	16-Jun-2004	BCSC	BCSC396	-	EU119597	658
-	OUTGROUP	*Spilosoma vagans*	CAN: BC: 11km SSW Elko	Schmidt, B. C.	18-May-2004	BCSC	BCSC84	-	n/a	658

* BCSC - B.C. Schmidt collection, Ottawa, Ontario ; BIO - Biodiversity Institute, University of Guelph, Guelph, Ontario; CNC - Canadian National Collection, Ottawa, Ontario; CSU - C.P. Gillette Museum of Arthropod Diversity, Colorado State University, Colorado; DHC - Daniel Handfield Collection; RBCM - Royal British Columbia Museum, Victoria, British Columbia; UASM - Strickland Entomological Museum, University of Alberta, Edmonton, Alberta; UCB - Essig Museum of Entomology, Univ. of California, Berkeley, California; USNM - National Museum of Natural History (formerly United States National Museum), Washington, DC.

** Some accession numbers not available at time of writing.

Appendix 2-2. Morphological and non-morphological characters of *Grammia* species used in phylogenetic analysis.

1. Females not attracted to light (0), attracted to light (1).

2. Males not attracted to light (0), attracted to light (1).

3. Thoracic vestiture of females appressed (0), loose (1).

4. Patagia scale colour: white form absent (0), present (1) [Fig. 2-37].

5. Thoracic scale colour of males: dark form absent (0), present (1) [Fig.2-28e].

6. Antennae mostly or entirely dark scaled (0) [e.g. Fig. 2-29], pale scaled (1) [Fig. 2-32a].

7. Male antennal pectinations: less than 3x segment length (0) [Fig. 2-1b, 2nd from top], greater than or equal to 3x segment length (1) [Fig. 2-1b, top].

8. Hindwing never with antemedial spots (0) [e.g. Fig. 2-10], at least occasionally with medial spots (1) [Fig. 2-8].

9. Hindwing with red scales (including oranges and pinks) never present (0) [Fig. 2-9], at least occasionally present (1) [Fig. 2-8].

10. Hindwing subterminal markings never interrupted by pale vein lines (0) [Fig. 2-7], at least occasionally interrupted by yellow vein lines (1) [Fig. 2-4].

11. Distal half of forewing never with vein lines (0) [Fig. 2-7], at least occasionally present (1) [Fig. 2-5].

12. Distal half of forewing not variable for vein lines (0) [Fig. 2-7], vein lines variably present, absent, or reduced (1) [Figs. 2-36, 2-37].

13. Forewing vein lines never fully developed, but basal third of anal vein pale line: absent (0) [Fig. 2-28e], present (1) [Fig. 2-34].

14. Forewing underside without distinct pink cast (0), with distinct pink cast (1).

15. Forewing markings of female similar to male (0) [Fig. 2-8b], highly reduced or absent (1) [Fig. 2-7b].

16. Forewing subterminal band of male always present (0) [Fig. 2-8], often highly reduced or absent (1) [Fig. 2-17a].

17. Forewing PM band with costal portion straight (0) [Fig. 2-8], curved basad (1) [Fig. 2-22].

Appendix 2-2 (cont'd.). Morphological and non-morphological characters of *Grammia* species used in phylogenetic analysis.

18. Forewing PM band curved or angled (0) [Fig. 2-8], linear (1) [Fig. 2-7].

19. Forewing M band meeting margin at acute angle (0) [Fig. 2-5], 90 degrees or greater (1) [Fig. 2-30].

20. Forewing M band linear (0) [Fig. 2-8], curving towards base at costa (1) [Fig. 2-22].

21. Forewing costal distance between base and M greater than between M and PM (0) [Fig. 2-6], equal (1) [Fig. 2-7a].

22. Forewing never with both basal and AM band fully developed (i.e. reaching at least to postcubital band) (0) [Fig. 2-30], at least occasionally with both basal and AM band extending to or beyond postcubital (1) [Fig. 2-37].

23. Forewing basal band never present (0)[Fig. 2-8], at least occasionally present (1) [Fig. 2-37].

24. Forewing never with more than one transverse band extending beyond postcubital stripe (0) [Fig. 2-18], at least sometimes with two or more bands extending through postcubital stripe (1) [Fig. 2-19].

25. Forewing costal cell entirely or predominantly dark scaled (0) [Fig. 2-8], pale scaled (1) [Fig. 2-4].

26. Forewing basal band never present (0) [Fig. 2-17], at least occasionally present (1) [Fig. 2-19].

27. Forewing anal margin with complete pale band (0) [Fig. 2-8], incomplete, thin marginal line, or absent (1) [Fig. 2-19].

28. Male vesica with diverticulae and vesical chambers not well differentiated (0) [Fig. 2-43b], well differentiated (1) [Fig. 2-41b].

29. Female ductus bursae primarly membranous (0) [Fig. 2-72], sclerotized (1).

30. Male aedeagus lacking apical sclerotized flap (0), with apical flap (1).

31. Male aedeagus lacking spines or spinules near apex (0), with spines or spinules near apex (0).

32. Male saccular process absent (0), present (1).

33. Female ductus bursae narrow and poorly differentiated from corpus bursae (0) [Fig. 2-74], enlarged and well-differentiated from corpus bursae (1).

Appendix 2-2 (cont'd.). Morphological and non-morphological characters of *Grammia* species used in phylogenetic analysis.

34. Distal portion of male valve below saccular extension: highly reduced (0) [Fig. 2-42a], flattened and elongate or rounded (1) [Fig. 2-4aa].

35. Male process of uncus with medial constriction absent (0) [Fig. 2-42a], present (1).

36. Dorsal margin of juxta convex (0), concave (1).

37. Juxta as wide or wider than length (0) [Fig. 2-40a], longer than wide (1) [Fig. 2-42a].

38. Pupal cremaster elongate (0), short and rounded (1).

39. Pupal lateral cremastral spines absent (0), present (1).

40. Pupal cremaster with longitudinal ridges lacking (0) with longitudinal ridges (1).

41. Larval warts with long setae only (0), with short and long setae (1).

42. Larval warts shiny (0), dull (1).

43. Larval dorsal abdominal setae finely barbed (0), coarsely barbed (1).

Appendix 2-3. Morphology character matrix.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
Grammia arge	1	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	1	0	1	0	1	0	1	1	1	1	0	1	0
Grammia doris	1	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	1	0	1	0	1	0	1	1	1	1	0	1	0
Grammia phyllira	1	1	0	0	0	0	1	0	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia favorita	0	1	0	0	0	0	1	?	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia placentia	1	1	0	0	0	0	1	0	1	0	0	0	1	1	0	0	1	1	0	1	0	0	0	0	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia virgo	1	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	1	0	0	1
Grammia anna	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia parthenice	1	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia virguncula	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia philipiana	1	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	?	?	?	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia kodara	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia quenseli	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia margo	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia franconia	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia figurata	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia f-pallida	1	1	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia incorrupta	1	1	0	1	1	0	1	0	1	0	0	0	0	0	0	1	0	1	1	0	1	0	1	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia allectans	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	1	0	1	0	1	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia ursina	1	1	0	0	1	0	1	0	1	0	0	1	0	0	0	1	0	1	1	0	1	0	1	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia nevadensis	0	1	0	0	1	0	1	1	1	0	0	0	0	0	0	1	0	1	1	0	1	0	1	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia behrii	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	1	1	0	1	0	1	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia eureka	0	0	0	0	0	0	0	?	1	0	0	0	0	0	0	1	0	1	1	0	1	0	1	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia brillians	?	1	0	0	1	0	1	?	1	0	0	0	0	0	0	1	0	1	1	0	1	0	1	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia bowmani	0	1	0	0	1	0	1	1	1	0	0	0	0	0	0	1	0	1	1	0	1	0	1	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia williamsii	0	1	0	0	1	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia elongata	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	1	0	0	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia blakei	0	1	0	0	0	1	1	1	1	0	0	1	0	0	0	1	0	0	1	0	1	0	1	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia cervinoides	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	1	0	1	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia fergusoni	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	1	0	1	0	1	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia ornata	1	1	0	1	0	0	1	1	1	1	1	0	0	0	0	1	0	1	1	0	1	0	1	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia hewletti	?	1	0	1	0	0	1	1	1	1	1	0	0	0	0	1	0	1	1	0	1	0	1	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia complicata	?	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	1	1	0	1	0	0	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia edwardsii	0	0	0	0	0	1	0	?	1	1	0	0	0	0	0	1	0	1	1	0	1	0	0	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Grammia yavapai	?	1	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	1	1	0	1	0	0	1	1	0	1	1	0	0	1	0	1	0	1	0	2	1	0	0	0	0	1
Holarctia obliterata	1	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	?	1	0	0	0	0	0	1	0	0	1	2	0	1	0	0	0	0	1	0	1	2	1	0	0	0	1

Chapter 3.

Rampant mtDNA introgression in *Grammia* tiger moths (Noctuidae: Arctiinae): broad-scale decoupling of organellar DNA and genomic integrity

INTRODUCTION

Hybridization among animal taxa has generally been viewed as rare in comparison to plants, with approximately 10% of animal species reported to hybridize with at least one other species, compared to 25% of plant species (Mallet 2005). Hybridization and gene introgression play a crucial and often controversial role in defining species concepts and understanding speciation (Coyne and Orr 2004), and the view that hybridization is unnatural or extremely rare among animals is perhaps best exemplified by the biological species concept (Mayr 1963), where hybridization is viewed as a breakdown of reproductive isolation, thereby challenging the integrity of a biological species. However, mounting genetic evidence shows that interspecific gene flow as a result of hybridization is not only more common than previously thought (*contra* Mayr 1992), but also that these phenomena play important adaptive roles (e.g. Sperling 1990, Boakye and Meredith 1993, Bull et al. 2006). This has resulted in modifications to the strict biological species concept, wherein hybridization and genetic exchange are accommodated in species definitions for animals (Mallet 1995; Sperling 2003; Claridge 2007).

Mitochondrial DNA (mtDNA) sequence data have often been used to study hybridization, particularly in conjunction with geographic data (Carr et al. 1986; Dowling and Demarais 1993; Sperling 1993b; Gardner 1996; Bull et al. 2006). Also, the utility of mtDNA sequences as phylogenetically informative characters in phylogeography, population ecology, systematics and taxonomy has contributed significantly to these disciplines. The functional and cellular characteristics of mtDNA are particularly amenable to phylogenetic analysis, since mtDNA genes are clonally inherited, non-recombining, fast-evolving and abundant (Simon et al. 1994). Furthermore, since mtDNA is maternally inherited, there should be greater congruence between species boundaries and mtDNA haplotypes in groups where the female is the heterogametic sex (such as the Lepidoptera; Sperling 1993a). This follows from Haldane's rule, where sterility or inviability is more frequent in heterogametic than homogametic hybrids (Haldane 1922; Coyne and Orr 2004), thereby decreasing the probability that non-native mtDNA will introgress into the native mtDNA gene pool. Mitochondrial DNA markers provide a valuable character set across a wide range of insect divergences, and have been successfully applied at a number of taxonomic levels, ranging from intraspecific variation to family-level phylogenies (Caterino et al. 2000). The cytochrome oxidase I and II (*cox1-2*) gene regions have proven particularly useful in delimiting taxonomically problematic species, particularly in the Lepidoptera (Caterino et al. 2000, Sperling 2003). Recent initiatives to compile a genetic barcode data bank based on part of the *cox1* gene (Hebert et al. 2003) reflect the capability of this marker as a tool for species diagnosis, although this approach is not without its limitations (Will and Rubinoff 2004; Hurst and Jiggins 2005; Monaghan et al. 2006).

Despite these useful qualities of mtDNA as a taxonomic tool, several causes can result in mtDNA variation that is discordant with average gene or species phylogenies; namely, mtDNA polyphyly can result from imperfect species taxonomy, hybridization, paralogous pseudogenes, incomplete lineage sorting, retained ancestral polymorphisms, insufficient phylogenetic signal and vertically transmitted symbionts. Reviews of these processes and their consequences are provided by Funk and Omland (2003) and Hurst and Jiggins (2005). As demonstrated here, species of *Grammia* tiger moths exhibit an extraordinary example of mtDNA sequence variation that is best explained by hybridization between multiple species pairs, followed by subsequent, extensive introgression. Remarkably, haplotypes are shared or are very similar between multiple species pairs that non-molecular characters (morphology, ecology, phenotype and behavioural characters; Chapter 2) show to be *not* closely related; conversely, single species exhibit divergent mtDNA lineages highly discordant with species as delimited by all other lines of evidence. This discrepancy between species boundaries (as inferred from non-molecular traits) and mtDNA genealogy demonstrates that genomic integrity in *Grammia* tiger moths is decoupled from mitochondrial phylogeny. Despite this taxonomically widespread discordance between gene and species phylogeny, species definitions that incorporate interspecific genetic exchange can accommodate extreme examples of mtDNA introgression like that observed in *Grammia*.

Grammia Rambur is the largest genus of tiger moths (Noctuidae: Arctiinae, *sensu* Lafontaine and Fibiger 2006) in the northern temperate region, and includes 36 species, all but three of which are restricted to North America (Chapter 2). The taxonomy of *Grammia* species has been revised using a 'total evidence' approach, wherein species boundaries are supported by morphology, ecology, biogeography, and behaviour (Chapter 2). All *Grammia* species have distributions that overlap with at least one other congener, and four or five species commonly occur in sympatry in appropriate habitats across broad geographic regions (Chapters 1, 2). The genus is distributed across all North American ecoregions, although the greatest species diversity occurs in western grassland and woodland biomes (Chapter 2).

The purpose of this chapter is to examine in detail the evidence for mtDNA polyphyly and haplotype introgression among multiple species of a relatively large and diverse genus of Lepidoptera. The species level taxonomy of *Grammia* used here is based on the 'total evidence' approach as presented in Chapter 2. I evaluate the possible causes of mtDNA polyphyly and other patterns of discordant variation, based on previously documented evolutionary and population genetic processes. Specifically, I examine how mtDNA variation discordant with species boundaries can be explained in light of geographic structure.

METHODS AND MATERIALS

Sampling

Two-hundred and seventy-seven specimens were obtained through field collections carried out in western Canada, recently collected museum specimens, and specimens obtained through other contributors (Appendix 2-1). Adult moths were collected with ultraviolet light traps, and freshly killed specimens or legs thereof were frozen at –20 °C or –70°C, or were placed in 99% ethanol prior to storage at –70°C if freezer facilities were not immediately available. Additional mtDNA sequence data (Appendix 2-1) were made available by contributors to the "All Leps Barcode of Life Campaign" at the University of Guelph (www.lepbarcoding.org). Species range maps were composed from distribution maps of examined specimens (Chapter 2), in addition to the distributional data of Ferguson et al. (2000).

Molecular techniques

Molecular variation was assessed based on the 658 bp barcode region of the cytochrome oxidase I (*coxI*) gene of the mitochondrial DNA genome (Hebert *et al.* 2003). The barcode region corresponds to nucleotide positions 1490–2198 of the *Drosophila yakuba* mitochondrial genome (Clary and Wolstenholme 1985). One to two legs of dried, fresh frozen or ethanol-preserved specimens were sent to the University of Guelph in dry Eppendorf tubes, and processed as part of the "All Leps Barcode of Life Campaign" (www.lepbarcoding.org). DNA extraction, amplification and sequencing protocols for the Barcode of Life initiative are detailed in Hebert et al. (2003).

A subsample of 26 specimens (19 species) was sequenced for the 770 bp region of *coxI* adjacent to the barcode region, using the primers Jerry (CAACATTTATTTTGATTTTTTGG; C1-J-2183 of Simon et al. 1994) and Pat II (TCCATTACATATAATCTGCCATATTAG; L2-N-3014 of Simon et al. 1994). Genomic DNA was extracted from legs of specimens using the QIAamp DNA Mini Kit (250) (Qiagen, Valencia, CA), and amplified through the Polymerase Chain Reaction (PCR) with heterologous primer pairs. PCR reactions were carried out using a Whatman Biometra TGradient or TPersonal Thermocycler (Whatman Biometra, Göttingen, Germany), with an initial denaturation cycle of 2 min at 94°C, followed by 35 cycles of 94°C for 30 s, 45°C for 30 s, 72°C for 2 min, and a final extension at 72°C for 5 min. The QIAquick PCR Purification Kit (250) (Qiagen, Valencia, CA) was used for cleaning PCR products, which were cycle-sequenced on either a Whatman Biometra TGradient or TPersonal Thermocycler using Amersham Bioscience DYEnamic ET Dye Terminator Kit (Amersham Biosciences, Buckinghamshire, England) using the following profile:

initial denaturation at 93.0°C for 30 s, 28 cycles of 95°C for 20 s, 45°C for 15 s, 60°C for 1 min, with a final extension at 60°C for 30 s. The sequenced product was purified through Sephadex column filtration (Amersham Biosciences, Uppsala, Sweden), then dried and re-suspended in formamide. Sequences were obtained using an ABI 377 automated sequencer (Applied Biosystems, Foster City, CA). All fragments were sequenced in both directions and manually aligned using Sequencher 4.1 (Gene Codes Corp. 2001).

DNA sequence analysis

Barcode region sequences were available for the two species of the subgenus *Mimarctia,* as well as 26 species of the subgenus *Grammia* (Chapter 2). Incomplete sequences were included only if more than 490 of 658 bp were available. A subsample of 19 species (1 subgenus *Mimarctia,* 18 subgenus *Grammia*) was sequenced for the barcode + Jerry-Pat regions. Haplotypes of all *cox1* sequences were initially compared with phylograms constructed using the neighbour-joining method in PAUP 4.0*b10 (Altivec) (Swofford 2001). Phyletic distances were calculated using the Kimura-2-Parameter (K2P) distance model. Phylogenetic signal of the two *cox1* fragments was compared using maximum parsimony (MP) phylogenetic analysis implemented in PAUP 4.0*b10, using heuristic searches with the following parameters: 100 random addition replicates; stepwise addition; tree bisection-reconnection (TBR). Branch support was calculated using bootstrap support values, obtained through 100 bootstrap replicates using the heuristic search methods given above.

Testing for geographic structuring of molecular variation using a nested clade analysis allows for important inferences to be drawn regarding intraspecific population structure, such as gene flow and historic events (Templeton et al. 1995). In a multi-species model, testing for geographic structure in mtDNA variation using this statistical approach would be useful in determining causes of mtDNA non-monophyly, since hybridization is expected to result in geographically structured mtDNA variation (Currat and Excoffier 2007), while neither retained ancestral polymorphic mtDNA (Masta et al. 2002) nor symbiont-mediated mtDNA variation (Jiggins 2003) are expected to. Due to the extent of shared haplotypes and low interspecific variation among multiple species, I was able to carry out a nested clade analysis for one of the major lineages evident in the neighbour-joining and maximum-parsimony phylograms (Eastern Lineage, Figs. 3-1, 3-6), using TCS 1.21 (Clement et al. 2000), and GeoDis 2.5 (Posada and Templeton 2006). The second lineage exhibiting extensive non-monophyly (Western lineage, Figs. 3-1, 3-2) consisted of haplotypes that were too divergent for nested clade analysis. TCS 1.21 was used to construct a haplotype network with a 95% confidence limit for parsimony (Templeton et al. 1995). Nesting structure was determined manually following the nesting rules given by Templeton et al. (1987). GeoDis 2.5 was used to assess geographic associations of the nested clades, using the network generated by TCS 1.21 and the geographic co-ordinates of the collection localities (Appendix 2-1). Although cladistic analysis of genetic and geographical data using GeoDis was designed for determining population structure and history of a single species (Templeton et al. 1995), this method is still useful for interpreting the geographic patterns of gene flow evident here, despite the obvious limitations of attempting to infer population structure and history of several species simultaneously. As detailed by Templeton et al. (1995), two types of statistical tests for geographic association are most useful for inferring population structure using a nested clade structure: *1)* a categorical test, which does not incorporate geographic information but instead treats sampling sites as categorical variables, and *2)* analysis using geographical distances. Both tests are implemented in GeoDis (Posada et al. 2000), and reported in Table 3-2 as the permutational contingency test (categorical), and geographic distance analysis. The latter assesses two distance measures for each clade: the average geographic distance of haplotypes from the clade center (D_c), and the average distance of all haplotypes from the *nesting* clade center (D_n) (Templeton et al. 1995). The nesting clade is defined as the clade that contains all those smaller clades that are removed from each other by one mutational step, as determined by the haplotype network. D_c is therefore a measure of how geographically widespread haplotypes from a given clade are, while D_n is the distance of all clade haplotypes from all haplotypes in the nesting clade (Templeton et al. 1995). Two probabilities are then calculated for each D, indicating whether or not D is significantly small or significantly large. The inference key for the results of the nested geographical clade analysis is given in Templeton et al. (1995).

RESULTS

I obtained *cox1* sequences for 28 of the 36 *Grammia* species currently recognized (Table 3-1). Phylogenetic analysis resolved 153 haplotypes among 274 specimens, which segregated into 13 lineages (Fig. 3-1). Although 11 of 13 lineages largely or exclusively correspond to nominal species, only nine of 28 species formed non-overlapping clusters in a neighbour-joining tree (Table 3-1; Fig. 3-1). Of the nine species exhibiting discrete haplotype clusters, minimum between-species divergence ranged from 2.97% to 8.96% (K2P model, Table 3-1). Two lineages, designated the Western and Eastern lineage, contained polyphyletic assemblages of 13 and ten species, respectively (Figs. 3-2, 3-3, 3-6). Patterns of non-monophyly were restricted to members of the subgenus *Grammia*, and there was no evidence of polyphyly within the subgenus *Mimarctia* (Fig. 3-1).

Of the subgenus *Grammia*, only seven of 26 species (*G. allectans G. anna, G. incorrupta, G. kodara, G. phyllira, G. placentia,* and *G. ursina*) exhibited discrete lineages; the remaining 19 species exhibited non-discrete lineages, 15 of which had at least one haplotype shared among two or more species (Table 3-1, Figs. 3-1, 3-2, 3-3). Within-species divergence was unusually large (>2.5%) in three species as a result of membership in multiple lineages (Table 3-1). Notably, none of the 53 *G. virguncula* sequence samples from across the species' range differed by more than four out of 658 bp from another species, despite having a diverse and divergent haplotype complement (Figs. 3-2b, 3-3). All other species with haplotypes restricted to the Eastern lineage (*G. figurata, G. f-pallida, G. margo, G. franconia, G. favorita)* were similar in this respect, with no haplotypes differing by more than one or two mutational steps from haplotypes of non-conspecifics (Fig. 3-3). However, small sample sizes for these five species could mean haplotypes with greater between-species divergence were simply not sampled.

The Virgo lineage included all but two of the *G. virgo* samples, with one each in the Kodara (Fig. 3-1) and Western lineages (Fig. 3-2). *Grammia parthenice* haplotypes fell into two lineages, the monophyletic Parthenice lineage, and the Eastern lineage (Figs. 3-1, 3-2). Of the 20 species with non-monophyletic haplotypes, 15 had haplotypes restricted to the Western and/or the Eastern lineage. *Grammia williamsii* and *G. quenseli* exhibited both eastern and western lineage haplotypes, in addition to the Kodara lineage (haplotypes WI1 and QE1 repsectively; Fig. 3-1).

Western lineage

Eight species had mtDNA that was restricted to the Western lineage, all of which are members of the *nevadensis* species-group (Ferguson and Schmidt 2007, Chapter 2), with an additional five species (*williamsii, elongata, virguncula, virgo, quenseli*) also exhibiting haplotypes outside of the Western lineage (Figs. 3-1, 3-3). Interspecific haplotype sharing occurred between the following species pairs or triplets: *bowmani-williamsii*, *blakei-williamsii*, *behrii-nevadensis*, *yukona-quenseli* and *elongata-ornata-complicata* (Fig. 3-2). Of the species restricted to the Western lineage, only *G. brillians* shared no haplotypes with other species, although the *brillians* haplotype (BR1) differed only by five mutational steps from *G. williamsii* haplotype WI4 (Fig. 3-2a). *Grammia williamsii* exhibited multiple haplotypes in both the Western and Eastern lineages (Figs. 3-2, 3-3), with Western haplotypes restricted to western North America and Eastern haplotypes occurring across the boreal region (Fig. 3-4e).

The Western lineage consisted of a total of 48 haplotypes, separated by a maximum of 50 mutational steps (Fig. 3-2). Species with multiple haplotypes (*G. williamsii, ornata, behrii, bowmani, elongata* and *nevadensis*) did not form monophyletic clusters, although both *G. ornata* and *williamsii* showed some haplotype subsets relatively distant from other haplotypes: the OR5-8 cluster of *ornata* (Fig. 3-2b, bottom) was segregated by a minimum of seven steps, while the WI12-13 cluster of *G. williamsii tooele* was segregated by at least 9 steps (Fig. 3-2, bottom right).

Eastern lineage

The Eastern lineage consisted of 34 haplotypes among 10 species. Five species displayed haplotypes restricted to the Eastern lineage, namely *G. figurata, G. f-pallida, G. margo, G. franconia* and *G. favorita* (Fig. 3-3). Nine of 34 haplotypes were shared among two or more species (Fig. 3-3), with the following species sets sharing haplotypes: *virguncula-parthenice, virguncula-parthenice-margo, virguncula-quenseli-franconia-williamsii, virguncula-williamsii, virguncula-elongata-margo-williamsii, virguncula-*

figurata, and *franconia-williamsii* (Fig. 3-3). All species with eastern lineage haplotypes shared at least one haplotype with another eastern lineage species, with the exception of *G. favorita* (one specimen sequenced) and *G. f-pallida* (two specimens sequenced).

Eastern lineage – nested clade analysis

The nested haplotype network revealed a maximum of 18 mutational steps among all haplotypes; the entire network consisted of 18 one-step clades, seven 2-step clades, four 3-step clades and two 4-step clades (Fig. 3-3). *Grammia williamsii, G. virguncula, G. elongata* and *G. quenseli* all exhibited haplotypes in both the Western and Eastern lineages (Figs. 3-2, 3-3). Geographic overlays of sampling sites and haplotypes by one- and two-step clades revealed recurring geographic patterns: among one-step clades, three showed a boreal-transcontinental distribution (I-7, I-8, I-17; Figs. 3-5b,c), while five clades were restricted to the northeastern / Atlantic region (I-6, I-13, I-14, I-15, I-16; Figs. 3-5b,c). Where two-step clades revealed additional significant geographic structuring, one clade remained segregated in the Atlantic region (II-3; Fig. 3-5b), and the central Great Plains / Great Lakes sampling sites formed clade II-5 (Fig. 3-5b), while one-step clades centered on the Appalachian region combined with boreal cades (clade II-4; Fig. 3-5b). Clades II-1 and II-2 indicated a central and northern transcontinental distribution, respectively (Fig. 3-5a), but lacked samples from the central continental region.

A nested contingency analysis confirmed significant geographic associations between geography and 10 of 20 nested clades (Table 3-2). Although most 1-step clades showed no significant geographic association, pooled 1-step clades at the second nesting level showed significant geographic associations in four of six clades (Table 3-2), likely reflecting lack of statistical power at the 1-step clade leve (Templeton et al. 1995). Historical or population structure inferences made based on these significant haplotype-geography associations using the inference key of Templeton et al. (1995) suggest 'past fragmentation', and 'contiguous range expansion' for the fourth level clades (Table 3-2).

Comparison of *cox1* fragments

Comparison of phylogenetic signal between the barcode and Jerry-Pat fragments revealed similar results with respect to monophyly of the western and eastern lineages, which were moderately to well-supported (Fig. 3-6). Topology within and outside of the western and eastern lineages differed substantially between the barcode and Jerry-Pat data sets, with the exception of clades with high bootstrap support (compare Fig. 3-6a and 3-6b). The Jerry-Pat region contained more variable sites as evidenced by longer branch lengths (Fig. 3-6). Combined *cox1* fragments showed unique haplotypes for each of the 26 specimens.

DISCUSSION

Species-level polyphyly (defined here to include both paraphyly and polyphyly) of mtDNA phylogenies is not infrequent; Funk and Omland (2003) report that 23% of species are polyphyletic, based on a survey of the published literature. A number of causes can result in gene tree polyphyly, as discussed by Funk and Omland (2003), each of which is evaluated below in light of the data presented here.

Inadequate phylogenetic information

Species-level polyphyly can result from inadequate phylogenetic signal when the length of mtDNA sequence does not contain enough variable, parsimony-informative sites to resolve relationships among closely-related species. The lack of phylogenetic resolution among *Grammia* with identical or similar haplotypes cannot be explained by lack of genetic signal, since moderate to deep divergences within the genus were evident (Fig. 3-1), and comparison of the 1357bp *cox1* combined fragment with the 658bp Barcode fragment revealed similar tree topologies, although the 700bp Jerry-Pat fragment downstream of the Barcode fragment contained more variable sites on average (Fig. 3-6). The high bootstrap support values for both the eastern and western lineages also indicate that lack of phylogenetic signal is not a problem.

Imperfect taxonomy

Polyphyly as a result of imperfect taxonomy implies that the mtDNA tree truly reflects the species tree, and that polyphyletic lineages are the result of *a*) a single variable species that has been 'oversplit' into multiple species, and/or *b*) multiple species that have been misdiagnosed as a single species as a result of species 'lumping'. The 'total evidence' approach to delimiting *Grammia* species (Ferguson and Schmidt 2007, Chapter 2) shows that differences are obvious and substantial for most of the *Grammia* species that exhibit polyphyletic patterns and shared haplotypes. Indeed, many species-pairs that share haplotypes are not closely related, according to non-molecular characters (Chapter 2). These include *G. williamsii-G. virguncula*, and *G. parthenice-G. margo*, and were particularly striking for *G. williamsii* and *G. virguncula*, which shared one or more haplotypes with nine and six species, respectively (Figs. 3-2, 3-3). Within the Eastern lineage, species thought to be closely related did not share haplotypes (*G. margo* and *G. franconia*, Fig. 3-3), while more distantly related species (based on morphological data) did share haplotypes, a pattern opposite to that expected under a species-oversplit model. The one exception to this is the possibility of a cryptic species within *G. virguncula*, currently treated as subspecies *G. virguncula speciosa*. Haplotypes representative of *G. v. speciosa* included eastern lineage haplotypes 7, 3, 11, 12, and 13 (Fig. 3-3, Appendix 2-1). If *speciosa* represents a distinct species, the extent of shared haplotypes would be even greater, since haplotypes 7 and 3 are also shared by nominate *G. virguncula* (3 and 7), *G. margo* (7) and *G. parthenice* (7) (Fig. 3-3).

Compared to the eastern lineage, the western lineage exhibited fewer shared haplotypes, but again imperfect taxonomy offers little in the way of explaining the observed broad patterns of polyphyly (Fig. 2). As in the eastern lineage, *G. williamsii* haplotypes occurred throughout the phylogram with three instances of shared haplotypes among a total of five other species. With the exception of two *G. ornata* lineages (OR5–8 and OR9-11) and one *G. williamsii* lineage (WI12-13), the western lineage exhibited very little molecular divergence (Fig. 3-2), despite containing 13 species, eight of which were restricted to this lineage. Based on the patterns of shared haplotypes, polyphyly, and species membership in multiple divergent lineages, clearly imperfect taxonomy cannot adequately explain mtDNA polyphyly in *Grammia*.

Paralogous genes

The presence of mtDNA genes integrated into nuclear DNA (mitochondrial pseudogenes) is generally rare, particularly so in insects. Pseudogenes are known from about 20 insect species, primarily Orthoptera, but have not been confirmed as occurring in Lepidoptera (Bensasson et al. 2001). The presence of pseudogenes in *Astraptes* skipper butterflies (Hebert et al. 2004a) has been discounted by Brower (2006). Although the presence of pseudogenes could explain limited cases of polyphyly at relatively low divergence levels, the large mtDNA divergences (2-3%) observed within some *Grammia* species cannot easily be explained by the presence of pseudogenes, since this would require very ancient mtDNA incorporation into the nuclear genome, especially in light of the fact that pseudogenes have much slower mutation rates compared to their mtDNA counterparts (Bensasson et al. 2001). Furthermore, none of the symptoms of pseudogene DNA contamination were evident in the processed samples, such as PCR ghost bands, base substitutions at normally conserved sites, sequence ambiguities between forward and reverse strands, and frameshift mutations (Bensasson et al. 2001).

Incomplete lineage sorting

Although it is difficult to demonstrate conclusively, the presence of retained ancestral polymorphic haplotype lineages can result in species-level polyphyly, as diverging species exhibit genealogies naturally progressing from polyphyly to paraphyly and eventually reciprocal monophyly, i.e. lineage sorting. Since the time it takes to progress to monophyletic lineages is dependent on population size, mtDNA is relatively robust to polyphyly among recently diverged species because mtDNA has an effective population size one-quarter that of nuclear DNA (Avise et al. 1987). Despite the difficulty in determining with certainty the occurrence of retained ancestral polymorphisms as a cause for polyphyly (particularly compared to gene introgression), polymorphisms should occur most commonly in closely-related species, but should be very rare in more distantly related species. More importantly, incomplete lineage sorting is not predicted to result in the geographic proximity of interspecifically shared haplotypes (Masta et al. 2002). The geographic distribution of *G. williamsii* (Fig. 3-4e) and *G. virguncula* (Fig. 3-4a) haplotypes, and of nested clades within the Eastern lineage

(Fig. 3-5), show clear spatial patterns. Geographic structuring would be expected with introgression resulting from hybridization, but not as a result of retained polymorphism. The incidence of shared or similar haplotypes among non-sibling species also renders incomplete lineage sorting as a highly improbable cause of polyphyly.

Despite the overall lack of evidence for lineage sorting, two exceptions are worth noting. Both *G. complicata-ornata-elongata* and *behrii-nevadensis* shared haplotypes (Fig. 3-2); *Grammia complicata / G. ornata* and *G. nevadensis / G. behrii* are believed to be sister species (Chapter 2), so it is possible that monophyly has not yet been achieved (although this alternative would be difficult to differentiate here from introgression among sibling species). *Grammia complicata* exhibited derived haplotypes with respect to *G. ornata,* a pattern consistent with "budding" or peripheral speciation (Harrison 1991). *Grammia complicata* is restricted to xeric habitats of southwestern coastal British Columbia and western Washington at the periphery of *G. ornata's* range, and is segregated from the nearest *G. ornata* populations by the Pacific rainforests (Chapter 2).

Interspecific hybridization

The transfer of mtDNA haplotypes from one species to another as a result of occasional interspecific mating can cause discordance between species- and gene trees. Mitochondrial gene trees may be particularly affected by introgression, since mtDNA is maternally inherited and can therefore reflect heterospecific origins; also, 'foreign' mtDNA can introgress further into the novel gene pool if it is less constrained by linkage to loci that are subject to selection, such as nuclear genes (Harrison 1990). The few cases where hybridization has been documented among multiple species within a genus suggest hybridization rates are relatively high in Lepidoptera. Between 6 and 15% of *Papilio* butterflies have documented hybrids (Sperling 1990), while Mallet et al. (2007) estimate species hybridization rates at 26-29% for heliconiine butterflies.

For hybridization to be a plausible mechanism causing mtDNA polyphyly, two requirements must be met: *1)* there must have been potential for cross-species contact (in both space and time), *i.e.* species must be para- or sympatric and synchronic; and *2)* reproductive isolating barriers must be incomplete, at least occasionally. Although evaluating the relative strengths of pre- and post-zygotic isolating mechanisms in

Grammia would be challenging, the fact that multiple haplotypes are shared between several non-sibling species across broad areas of sympatry seems to unequivocally point to mtDNA introgression as the primary mechanism resulting in polyphyly. Courtship and mating are poorly documented in *Grammia*, although mate attraction, courtship and mating sequence is no doubt similar to that of other arctiines (and noctuids); female pheromones function in long-distance mate attraction (e.g. *Grammia blakei;* Byers 1989) while close-range courtship can be mediated by male pheromones (e.g. Krasnoff and Roelofs 1989), and complex genitalic morphology may regulate structural compatibility (Häuser and Boppré 1997).

Structures associated with courtship are reduced or lost in *Grammia* tiger moths, a condition that almost certainly represents a secondary loss rather than a primitive state within the Arctiinae (Weller et al. 1999, Jacobson and Weller 2002). Namely, the male coremata used for courtship pheromone dissemination in the subtribe Arctiina (Krasnoff and Roelofs 1989, Krasnoff and Yaeger 1988) is highly reduced in *Grammia* (Ferguson 1985, Chapter 2), and the chemical precursor of arctiid male pheromones, hydroxydanaidal, is absent in *Grammia incorrupta* (Hartmann et al. 2005). The thoracic tymbal structure used for ultrasound production during courtship in other arctiine species (Krasnoff and Roelofs 1989, Krasnoff and Yaeger 1988) is also simplified in *Grammia* (Ferguson 1985, Chapter 2). It can therefore be inferred that *Grammia* courtship is most likely simplified, and appears to lack the components necessary for complex, species-specific mate interactions.

The species-specific genitalic morphology that acts as a mechanical pre-zygotic isolating mechanism in other Noctuidae (Byers and Hinks 1978, Lafontaine 1981, Lafontaine and Mikkola 1987, Mikkola 1992) is essentially absent in *Grammia*; rather, genitalic structure is highly conserved among species and species-groups, with subtle interspecific differences in morphology (with the exception of significant morphological differences between subgenera; Chapter 2). Conservative genitalic morphology suggests that structural incompatibility may not play an important role as an isolating mechanism. This concept is demonstrated rather well in *Euxoa* cutworm moths (Noctuidae). Species that are not necessarily closely related but show compatible male and female genitalia are able to hybridize, while closely related species with divergent genitalic structure are not (Byers and Hinks 1978, Lafontaine 1981).

Grammia females attract males with long-distance pheromones (Byers 1989). Occasional attraction of heterospecific males may occur in *Grammia*, a phenomenon documented in other arctiines, even among species that are not closely related (Roelofs and Cardé 1971, Clarke et al. 1996). The morphological, behavioural and ecological evidence therefore suggests that isolating barriers within *Grammia* are relatively porous, congruent with the observed genetic patterns of hybridization.

The surprising prevalence of identical or similar haplotypes among multiple species across large geographic regions shows not only that hybridization is taxonomically widespread, but that many species have undergone regional mitochondrial replacement. No Eastern haplotypes were detected in *G. williamsii* in the western core of the species' range (Fig. 3-4e), despite being present in most boreal and all eastern *G. williamsii* samples. Similarly, all boreal samples of *G. parthenice* were Eastern lineage haplotypes, with the Parthenice lineage centered on the southeast U.S. / Appalachian region (Fig. 3-4b). *G. elongata* (Fig. 3-4i) and *G. quenseli* (Fig. 3-4h) showed similar patterns, with samples from localities overlapping with other Eastern lineage species exhibiting Eastern haplotypes. It is important to note that shared haplotypes between more than two species does not require hybridization compatibility between all pairwise species combinations exhibiting that haplotype; haplotype sharing could be attained through limited pairwise crossings, resulting in a stepping-stone mechanism for a haplotype to attain multi-species membership. It should be possible to test this through extensive sampling of species membership for a given clade, such as II-7 (Fig. 3-3). The extent of hybridization within *Grammia* is particularly unexpected given that female hybrids should exhibit lower fitness than males, in accordance with Haldane's rule (Haldane 1922). Elimination of these hybrid females would therefore be expected to result in a disproportionate loss of hybrid-interaction mtDNA.

Due to the significant extent of interspecific haplotype sharing, inferences drawn from the geographical clade analysis are not straightforward, since this analysis was designed to discriminate among restricted gene flow and historical events (range expansion, long-distance colonization and population fragmentation) for populations of a single species (Templeton et al. 1995). Interpretation of historical events is dependent upon the assumption of adequate geographical sampling (Templeton et al. 1995). Past population fragmentation can clearly not be directly inferred for this data set. However, this inference is indicative of geographically fragmented, locally structured nested-clades, as would be expected under a hybridization scenario. In other words, the significantly small clade distances (D_c, Table 3-2) indicative of inferred past fragmentation (Templeton et al. 1995) would also be expected if conditions favouring hybridization were geographically restricted. This could explain the geographic association seen in clades I-18 and I-17, which were restricted to the northern Rocky Mountain and central boreal regions, respectively (Fig. 3-5c), despite the fact that each clade consisted of four species. Most importantly, categorical analysis revealed that multi-species mtDNA genealogy showed significant geographic structure patterns that are discordant with distributions of taxonomic entities, i.e. haplotypes of a single species did not generally form clades, while multi-species haplotypes often formed geographically restricted clades.

Although it may be impossible to elucidate species-specific population histories of the species hybridizing in the eastern clade, it is clear that the eastern clade haplotypes show a clustered or contagious geographic pattern. Haplotype sharing appeared to be less pervasive within the Western lineage. Differences in adult flight times among Western versus Eastern lineage species may help explain this pattern. Substantially greater temporal overlap occurs among Eastern lineage species, since flight times for most species are mid-spring to mid summer, and adults of multiple species often occur together during certain times of the season (Chapter 2). This would be an obvious prerequisite for hybridization events. Western lineage species exhibit either spring or early fall flight seasons, avoiding the hottest, driest part of the season throughout the Great Plains and intermontane regions. *Grammia williamsii, G. blakei, G. bowmani, G. elongata, G. ornata* and *G. complicata* are spring species (Chapter 2), while *G. nevadensis* and *G. behrii* fly in early fall. Haplotype sharing occurred within, but not among spring and fall species in the Western lineage, although haplotype clusters did not segregate into two (spring and fall) species clusters (Fig. 3-2).

Regional replacement of mtDNA

Two processes affecting mtDNA diversity could explain the geographically contagious pattern of haplotype sharing. First, selection acting on mtDNA (either direct or indirect) could result in selective sweeps with subsequent geographical replacement of haplotypes. A prevalent and perhaps underestimated indirect selection mechanism is the effect of vertically transmitted symbiotic bacteria, such as *Wohlbachia*. Hurst and Jiggins (2005) summarize examples of symbiont-infected strains of insect species associated with mtDNA haplotype lineages, and genetic consequences of symbiont infection. For example, Jiggins (2003) showed that *Wohlbachia* infection has resulted in loss of mtDNA diversity in some populations of *Acraea encedon* L. butterflies, and that mtDNA and *Wohlbachia* have introgressed from the closely related *Acraea encedana*. *Wohlbachia*, and some other symbionts, are able to bias the sex ratio of their hosts (e.g. through killing of male hosts during embryogenesis), since only female hosts transmit symbionts, along with mtDNA. *Wohlbachia* therefore typically occurs in disequilibrium with mtDNA in natural populations, resulting in the spread of symbiont-associated haplotypes following initial infection (Hurst and Jiggins 2005). A dramatic example of this has been documented in *Drosophila simulans* Sturtevant (Turelli et al. 1992). However, in order to explain the mtDNA patterns evident in *Grammia*, symbiont-associated mtDNA selection (or indeed other indirect selection mechanisms) would require multiple selective sweeps across broad geographic regions and taxonomic boundaries. Although bacterial symbionts such as *Wohlbachia* may well be affecting mtDNA diversity in *Grammia*, it is unlikely that this scenario would result in significant geographic structuring of mtDNA, since symbiont infection results in decreased geographic structuring of mtDNA (Jiggins 2003).

Alternatively, mitochondrial substitution could occur if there are large differences in abundance of hybridizing species (Chan & Levin 2005). Several factors, operating at different time scales, could bring about abundance differences among sympatric *Grammia* species. Differences in the peak of adult flight times (Chapter 2) would often result in abundance differences at any given time during the flight season, since species at the peak of their flight would be common relative to species at the periphery of their flight season. Year to year differences in abundance as a result of population fluctuations would most likely be species–specific; abundance discrepancies would be particularly pronounced if a species underwent occasional population explosions, such as those of *G. blakei* (Byers 1988).

As inferred from the nested geographical clade analysis, the large-scale geographic patterns of mtDNA complements could, at least in part, also be explained by historical events such as glacial and interglacial range contractions and expansions. Since *Grammia* species would undoubtedly exhibit differential post-glacial colonization patterns, colonizing species undergoing a range expansion would be rare compared to an established or resident species. Currat and Excoffier (2004) showed that expanding populations of species are likely to have their genome replaced by resident species, assuming hybrid viability. This process has been proposed to explain mitochondrial replacement in sibling bat species in Europe (Berthier et al. 2006), and may also explain discordance between nuclear and mtDNA phylogenies of Hawaiian crickets (Shaw 2002), European leaf beetles (Gómez-Zurita and Vogler 2003) and North American sawflies (Linnen and Farrell 2007).

The hypothesis of mtDNA introgression as a result hybridization between invader (rare) and resident (common) species, with subsequent mtDNA replacement, is congruent with the phylogeography of *Grammia* with Eastern lineage haplotypes. In the context of postglacial biogeography, this range expansion model requires differential colonization rates following deglaciation. The most likely candidate for a common 'resident' boreal species (and by implication the origin of the Eastern lineage haplotypes) is *G. virguncula*, based on this species' ecology, geographical distribution, and haplotype complement. *Grammia virguncula* occurs in a variety of grassland and tundra habitats, including subarctic tundra and boreal forest bogs (Chapter 2), and it is widespread and locally common throughout the boreal zone (Fig. 3-4a, Chapter 2). Moreover, extensive geographic sampling revealed that all but one of 53 *G. virguncula* samples were Eastern lineage haplotypes (Fig. 3-1, 3-3). The habitat preference and distribution of *virguncula* suggests that it would have been adapted to the cooler, boreal or tundra habitats of glacial refugia in relative proximity to the continental ice sheets (Schwert and Ashworth 1988, Pielou 1991). Western populations may have originated from a Beringian and a Great Plains refugium (Pielou 1991), given the geographic distribution of clades I-2 (Fig. 3-5a), I-18 (Fig. 3-5c), and differentiation into the western subspecies *G. v. celineata* (Chapter 2). Similarly, the unique haplotypes (clade I-6, Fig. 3-5b) and phenotypes (Chapter 2) occurring in the Atlantic maritime region provide further evidence of unique populations derived from a Newfoundland-Cape Breton-Gaspé refugium (Pielou 1991). Numerous other endemic insect species or subspecies have ranges that are indicative of this refugium (e.g. Hamilton & Langor 1987), including at least three butterfly species (Sperling & Harrison 1994, Layberry et al. 1998).

The evidence for range expansion followed by introgression of Eastern lineage haplotypes is strongest for two species, *Grammia williamsii* and *G. parthenice*. In *G. williamsii*, Western lineage haplotypes (presumably the native lineage) are prevalent in the core of the species' range in western North America, while Eastern lineage haplotypes occur throughout the boreal zone (Fig. 3-4e). This pattern could be explained by a postglacial range expansion from western grasslands into the boreal zone, where *williamsii* inhabits dry, open pine woodland (Chapter 2), ecologically similar to the xeric habitats of western North America. The presence of this species in New England (Fig. 3-4e) also leaves open the possibility of persistence in an East Coast maritime refugium, as discussed above. A phylogeographic pattern similar to that of *G. williamsii* is seen in *G. parthenice*, in that a unique and divergent lineage (Parthenice lineage, Fig. 3-1) is largely extralimital to the distribution of Eastern lineage haplotypes occurring in the boreal zone (Fig. 3-4b). This again suggests that *G. parthenice* mtDNA was replaced by Eastern haplotypes following colonization of the boreal region upon deglaciation.

Significance and Conclusions

The results presented here have a number of implications pertinent to phylogenetic analysis and evolutionary process. First, taxonomically and geographically extensive mtDNA introgression in *Grammia* compromises the ability of mtDNA gene trees to estimate species trees. Widespread mtDNA non-monophyly has obvious implications for barcode-based species identification (Hebert et al. 2003; Hebert et al. 2004a; Hajibabaei et al. 2006a, 2006b) but also highlights the dangers of interpreting sequence data based on incomplete taxonomic and geographic sampling. The mtDNA sequences of *Grammia* also document a noteworthy example of genetic diversity within and between species of a genus. Comparisons of within- versus between-species genetic variation initially suggested a lack of overlap in these parameters (e.g. Avise 1974, Satta et al. 1987, Brower & Boyce 1991), and this purported genetic gap in the variation of *cox1* has subsequently been proposed as a metric to identify species, most notably in the DNA "barcode" initiative (Hebert et al. 2003). This "barcode gap" (Meyer and Paulay 2005) should therefore aid in molecular species diagnosis, and species limits have been proposed at 3% minimum divergence (Hebert et al. 2003) or 10 times the average intraspecific divergence (Hebert et al. 2004b). Most (19/28) *Grammia* species exhibited haplotypes less than 1% divergent from one or more other species, and maximum within-species divergence was significantly greater than between-species divergence in nine of these 19 species (Table 3-1). A molecular approach to defining *Grammia* species, where non-overlap of within- versus between-species nucleotide diversity is important (Meyer and Paulay 2005), would therefore correctly diagnose only 19 of 28 (69%) species. Even when only those species with discrete haplotype clusters (i.e. non-overlap of within/between species divergence) are considered, there was no evidence of a break in genetic variation, since maximum within-species divergence values across the genus closely approached minimum between species differences (Table 3-1). Similarly, a recent review of DNA sequence difference among a wide variety of insect taxa shows that intra-/interspecific divergence overlap would result in misdiagnosis of 45% of examined taxa (Cognato 2006). Analytical methods statistically more powerful than distance comparisons, designed to overcome the diagnostic limitations imposed by genetic overlap (Abdo & Golding 2007), may resolve some of the molecular species-diagnostics complexities such as those observed in *Grammia*. However, these methods would still fail in the face of shared haplotypes among multiple species, a pervasive phenomenon in *Grammia* where 15 of 28 sampled species shared haplotypes with at least one other species.

Widespread cryptic hybridization among *Grammia* species challenges biological species concepts, even those in which hybridization is 'allowed'; previous evidence for natural hybridization in animals has primarily been limited to sibling species (reviewed by Mallet 2005 and Chan and Levin 2005) with geographically restricted gene introgression (but see Berthier et al. 2006). A notable exception to this is given by Linnen and Farrell (2007), who demonstrate discordant mtDNA and nuclear genealogies for *Neodiprion* sawflies resulting from rampant introgression among multiple non-sibling species, showing non-monophyletic patterns surprisingly similar to those seen in *Grammia*. Clearly, hybridization is not a phenomenon restricted only to recently diverged species. Data presented in this study suggest that four *Grammia* species (*williamsii, quenseli, elongata, virguncula*) exhibit haplotypes from at least two major lineages (Western and Eastern), differing by an average of approximately 5% (Table 3-1, Figs. 3-2, 3-3). Assuming a molecular clock rate of 2% divergence per million years (Brower 1994), these lineages diverged during the late Pliocene, approximately 2.5 mya. Species of the Western lineage likely represent a radiation in response to the late Miocene – early Pliocene expansion of the North American grasslands (Janis et al. 2004), since nearly all occur in xeric grassland or woodland habitats of western North America (Chapter 2).

The *cox1* mtDNA genealogy of *Grammia* tiger moths demonstrates that phylogenetic, taxonomic, and biogeographic interpretations based on mtDNA should be used with great caution, and not without independent character sets based on morphology, ecology, or nuclear markers. Conversely, mtDNA markers are invaluable for detecting cryptic hybridization. The notion that multiple, non-sibling species retain their genomic integrity in the face of rampant mtDNA introgression is particularly intriguing in light of evolution of mating barriers. Research on factors governing hybridization in *Grammia* would be particularly informative to understanding the role of isolating mechanisms in speciation.

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Table 3-1. Summary of tree topology data for *Grammia* species, based on the 658 bp Barcode region (Figure 3-1).

Species	Sample size	No. haplotypes	Clade membership	Max. haplo. membership†	Min. BSD††	Max. WSD★	Discrete haplo. clusters★★
Grammia (Mimarctia) arge	14	5	1	1	4.92	0.50	*
Grammia (") doris	3	2	1	1	4.92	1.23	*
Grammia (Grammia) allectans	1	1	1	1	3.78	-	*
Grammia (") anna	6	6	1	1	4.90	1.78	*
Grammia (") behrii	3	3	1	2	0.00	0.10	
Grammia (") blakei	2	1	1	2	0.00	0.00	
Grammia (") bowmani	2	2	1	2	0.00	0.15	
Grammia (") brillians	1	1	1	1	0.75	-	
Grammia (") complicata	4	3	1	3	0.88	0.85	
Grammia (") elongata	4	3	2	3	0.00	4.42	
Grammia (") favorita	1	1	1	1	0.15	-	
Grammia (") figurata	11	5	1	2	0.00	1.45	
Grammia (") f-pallida	2	1	1	1	0.30	0.00	
Grammia (") franconia	6	3	1	4	0.00	0.31	
Grammia (") incorrupta	4	4	1	1	2.97	2.33	*
Grammia (") kodara	2	2	1	1	2.70	0.70	*
Grammia (") margo	4	2	1	4	0.00	0.86	
Grammia (") nevadensis	22	11	1	2	0.00	2.89	
Grammia (") ornata	9	9	1	3	0.88	4.03	
Grammia (") parthenice	20	9	2	3	0.00	3.52	
Grammia (") phyllira	8	7	1	1	8.96	2.82	*
Grammia (") placentia	6	4	1	1	6.06	0.67	*
Grammia (") quenseli	8	5	3	4	0.00	10.98	
Grammia (") ursina	2	2	1	1	2.97	0.46	*
Grammia (") virgo	25	14	3	1	0.25	7.14	
Grammia (") virguncula	53	23	2	4	0.00	6.28	
Grammia (") williamsii	49	23	3	4	0.00	6.47	
Grammia (") yukona	2	1	1	1	0.63	0.00	
Total	274	153	-	-	-	-	10

† Maximum number of species sharing a haplotype occurring in a given species

†† Minimum between-species divergence (K2P model)

★ Maximum within-species divergence (K2P model)

★★ Species with discrete haplotype clusters, and at least 1% divergent from all other species

Table 3-2. Results for nested contingency analysis of geographical associations for all Eastern lineage *Grammia* samples, for the *coxI* Barcode region.

Clade	Permutational chi-sq	Nested clade	Dc★	Dn†	Dc [I-T]	Dn [I-T]	Inference chain	Inferred process
1-1	ns	-	-	-	-	-	1-NO	Inconclusive
1-2	ns	-	-	-	-	-		
1-4	ns	-	-	-	-	-		
1-5	ns	-	-	-	-	-		
1-7	ns	-	-	-	-	-		
1-11	ns	-	-	-	-	-		
1-12	ns	-	-	-	-	-		
1-17	0.002	11	-	-	-	S *	1-2-3-5-15-16-18-NO	Inconclusive
		12	-	-				
		23	-	-				
		24	S **	L **				
		26	-	-				
		31	-	-				
		32	-	-				
1-18	<0.001	20	S **	L **	L **	L **	1-2-3-5-15-NO	Past fragmentation
		21	S **	S **				
2-1	ns	-	-	-	-	-	1-NO	Inconclusive
2-2	0.013	1-3	-	S *	-	-	1-2-3-5-15-16-18-NO	Inconclusive
		1-4	S **					
		1-5	S **	L **				
2-4	<0.001	1-7	-	S **	-	-	1-2-3-5-15-NO	Past fragmentation
		1-8	S **	L **				
		1-9	-	-				
2-5	0.015	1-10	L **	L **	S **	S **	1-2-3-5-15-NO	Past fragmentation
		1-11	-	-				
		1-12	-	-				
2-6	ns	-	-	-	-	-	1-NO	Inconclusive
2-7	0.006	1-15	S *	-	-	-	1-2-3-5-15-NO	Past fragmentation
		1-16	-	-				
		1-17	S **	S **				
		1-18	L *	L **				
3-1	ns	-	-	-	-	-	1-NO	Inconclusive
3-2	<0.001	2-3	-	-	-	-	1-2-3-4-9-NO	Past fragmentation
		2-4	L *	L *				
		2-5	S **	S **				
4-1	<0.001	3-1	-	-	-	-	1-2-11-12-NO	Contiguous range expansion
		3-2	S *	-				
4-2	0.001	3-3	S **	S *	-	-	1-2-11-12-NO	Contiguous range expansion
		3-4	L **	L **				
total cladogram	<0.001	4-1	S **	S **	-	-	1-2-3-6-5-15-NO	Past fragmentation
		4-2	L *	L **				

★ Probability that Dc (Clade distance) or Dn (nested clade distance) is significantly large (L) or small (S), with a probability of 0.10 - 0.049 (*) and <=0.05 (**)

† Clade (Dc) and nested clade (Dn) distances for interior versus tip clade comparisons.

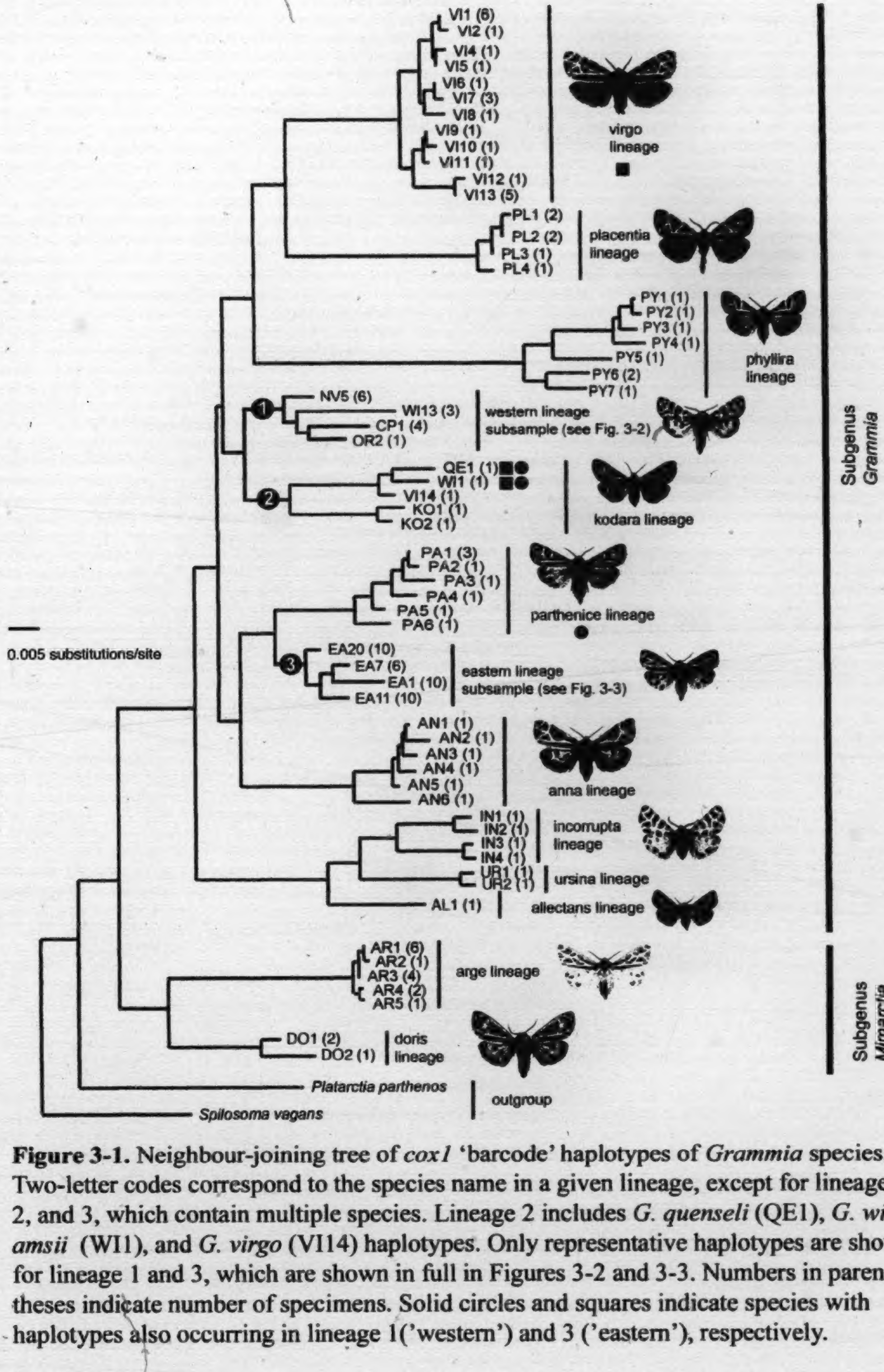

VI1 (6)
VI2 (1)
VI4 (1)
VI5 (1)
VI6 (1)
VI7 (3)
VI8 (1)
VI9 (1)
VI10 (1)
VI11 (1)
VI12 (1)
VI13 (5)
virgo lineage
■
PL1 (2)
PL2 (2)
PL3 (1)
PL4 (1)
placentia lineage
PY1 (1)
PY2 (1)
PY3 (1)
PY4 (1)
PY5 (1)
PY6 (2)
PY7 (1)
phyllira lineage
1
NV5 (6)
WI13 (3)
CP1 (4)
OR2 (1)
western lineage subsample (see Fig. 3-2)
QE1 (1) ■●
WI1 (1) ■●
VI14 (1)
KO1 (1)
KO2 (1)
2
kodara lineage
PA1 (3)
PA2 (1)
PA3 (1)
PA4 (1)
PA5 (1)
PA6 (1)
parthenice lineage
●
0.005 substitutions/site
3
EA20 (10)
EA7 (6)
EA1 (10)
EA11 (10)
eastern lineage subsample (see Fig. 3-3)
AN1 (1)
AN2 (1)
AN3 (1)
AN4 (1)
AN5 (1)
AN6 (1)
anna lineage
IN1 (1)
IN2 (1)
IN3 (1)
IN4 (1)
incorrupta lineage
UR1 (1)
UR2 (1)
ursina lineage
AL1 (1)
allectans lineage
AR1 (6)
AR2 (1)
AR3 (4)
AR4 (2)
AR5 (1)
arge lineage
DO1 (2)
DO2 (1)
doris lineage
Platarctia parthenos
Spilosoma vagans
outgroup
Subgenus Grammia
Subgenus Mimarctia

Figure 3-1. Neighbour-joining tree of *cox1* 'barcode' haplotypes of *Grammia* species. Two-letter codes correspond to the species name in a given lineage, except for lineages 1, 2, and 3, which contain multiple species. Lineage 2 includes *G. quenseli* (QE1), *G. williamsii* (WI1), and *G. virgo* (VI14) haplotypes. Only representative haplotypes are shown for lineage 1 and 3, which are shown in full in Figures 3-2 and 3-3. Numbers in parentheses indicate number of specimens. Solid circles and squares indicate species with haplotypes also occurring in lineage 1('western') and 3 ('eastern'), respectively.

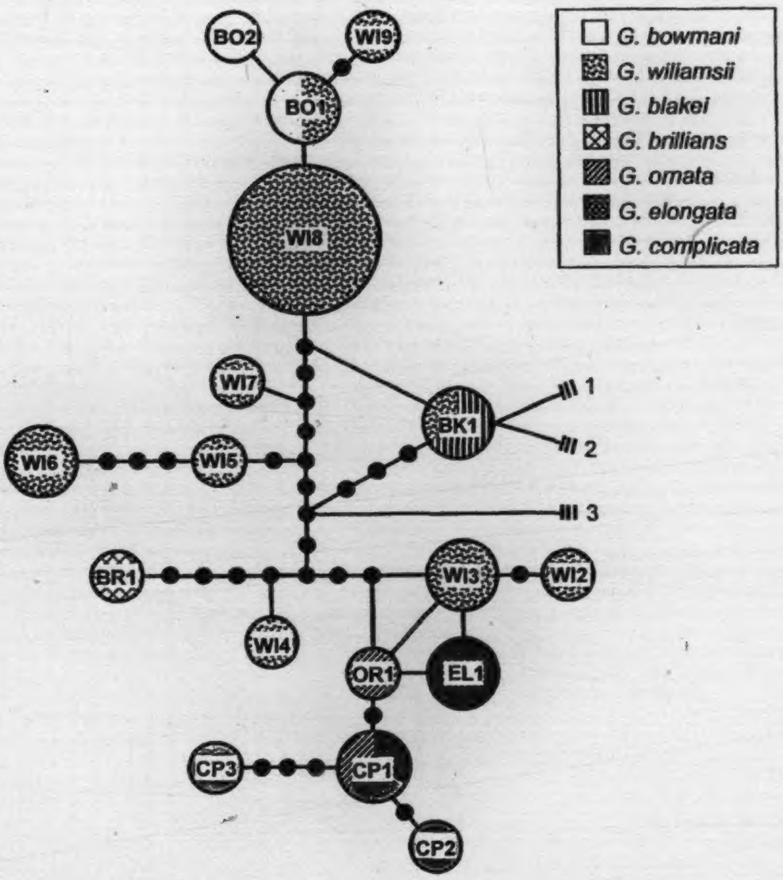
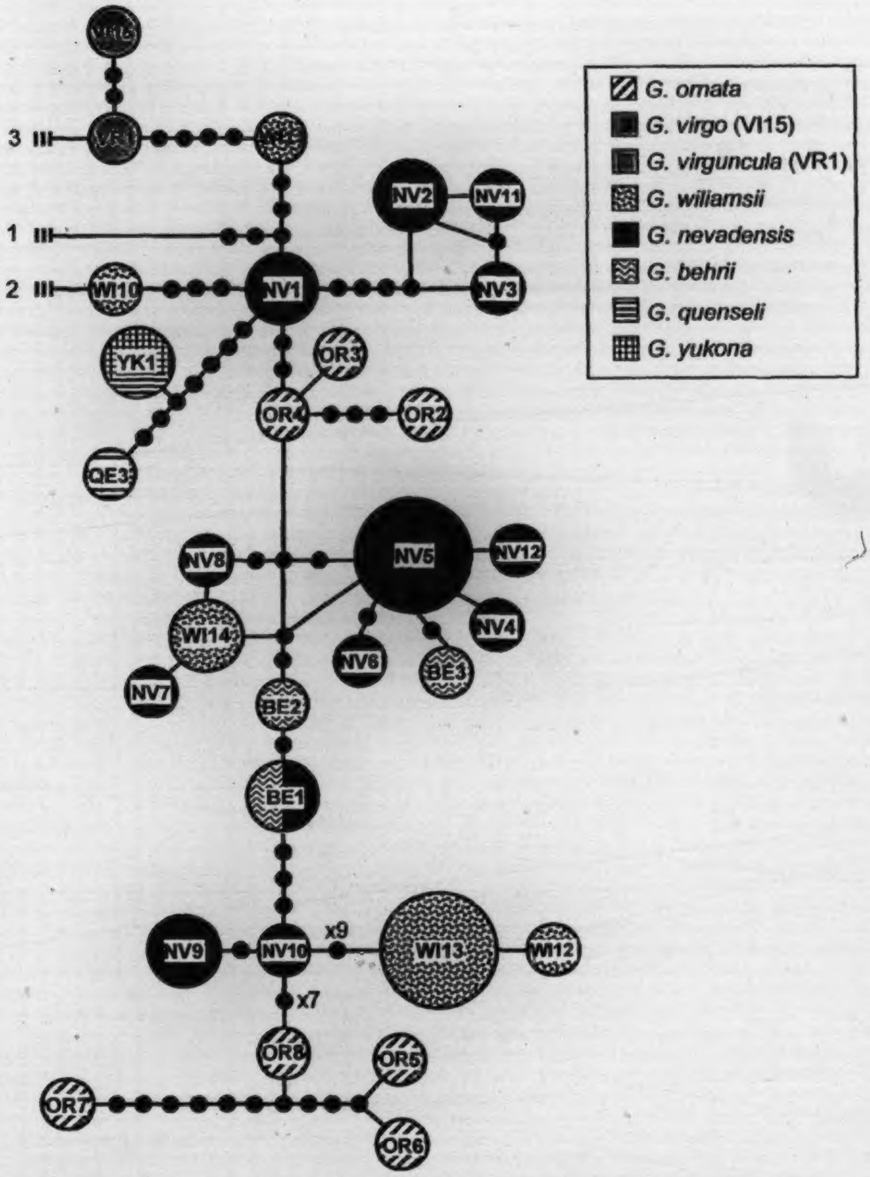

BO2
WI9
BO1
WI8
WI7
BK1
1
2
WI6
WI5
3
BR1
WI3
WI2
WI4
OR1
EL1
CP3
CP1
CP2
G. bowmani
G. williamsii
G. blakei
G. brillians
G. ornata
G. elongata
G. complicata

Figure 3-2a. Partial haplotype network of the 48 Western lineage haplotypes. Numbered circles indicate haplotypes, small solid circles an intermediate hypothetical haplotype connecting observed haplotypes; circle size corresponds to haplotype frequency, where small numbered circles = 1, medium = 2 to 4, large = 5 to 7, and largest 8 or more specimens. Lines between circles correspond to a one-step mutational change. Lines 1, 2, and 3 continue to remainder of haplotype network in Figure 3-2b.



▨ G. ornata
■ G. virgo (VI15)
■ G. virguncula (VR1)
▩ G. williamsii
■ G. nevadensis
▩ G. behrii
☰ G. quenseli
▦ G. yukona
VI15
3
VR1
NV2
NV11
1
2
WI10
NV1
NV3
YK1
OR3
OR4
OR2
QE3
NV8
NV5
NV12
WI14
NV4
NV6
BE3
NV7
BE2
BE1
NV9
NV10
x9
WI13
WI12
x7
OR8
OR5
OR7
OR6

Figure 3-2b. Partial haplotype network of the 48 Western lineage haplotypes. Numbered circles indicate haplotypes, small solid circles an intermediate hypothetical haplotype connecting observed haplotypes; circle size corresponds to haplotype frequency, where small numbered circles = 1, medium = 2 to 4, large = 5 to 7, and largest 8 or more samples. Lines between circles correspond to a one-step mutational change. Lines 1, 2, and 3 continue to remainder of haplotype network in Figure 3-2a. "x7" and "x9" indicate 7 and 9 mutational steps, respectively.

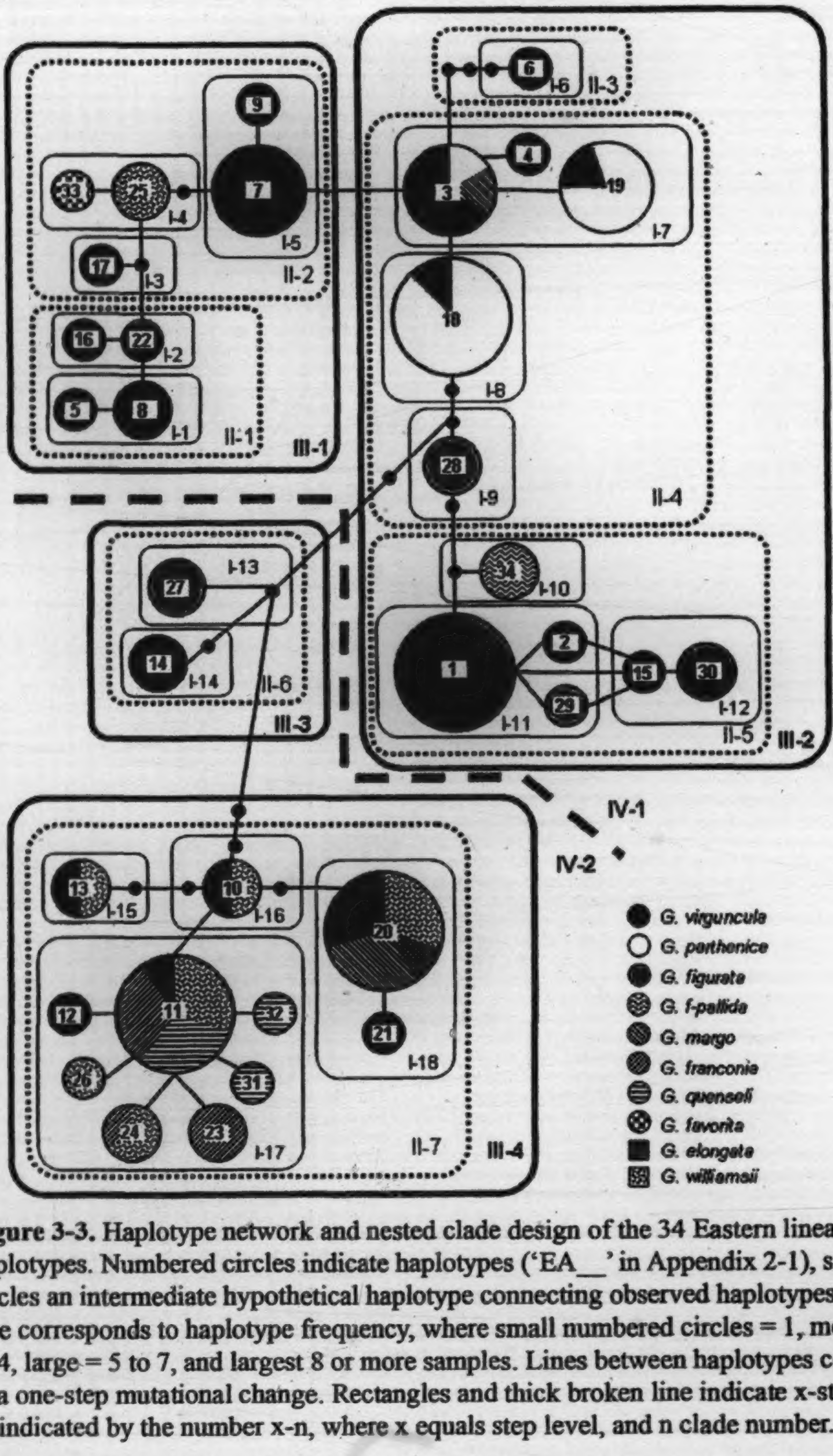

6
I-6
II-3
9
4
33
25
I-4
7
3
19
I-7
I-5
17
I-3
II-2
18
16
22
I-2
I-8
5
8
I-1
II-1
III-1
28
I-9
II-4
27
I-13
34
I-10
14
I-14
II-6
III-3
1
2
15
30
29
I-11
I-12
II-5
III-2
IV-1
IV-2
13
I-15
10
I-16
20
12
11
32
21
26
31
I-18
24
23
I-17
II-7
III-4
● G. virguncula
○ G. parthenice
● G. figurata
G. f-pallida
G. margo
G. franconia
G. quenseli
G. favorita
■ G. elongata
G. williamsii

Figure 3-3. Haplotype network and nested clade design of the 34 Eastern lineage haplotypes. Numbered circles indicate haplotypes ('EA__' in Appendix 2-1), small solid circles an intermediate hypothetical haplotype connecting observed haplotypes; circle size corresponds to haplotype frequency, where small numbered circles = 1, medium = 2 to 4, large = 5 to 7, and largest 8 or more samples. Lines between haplotypes correspond to a one-step mutational change. Rectangles and thick broken line indicate x-step clades, as indicated by the number x-n, where x equals step level, and n clade number.

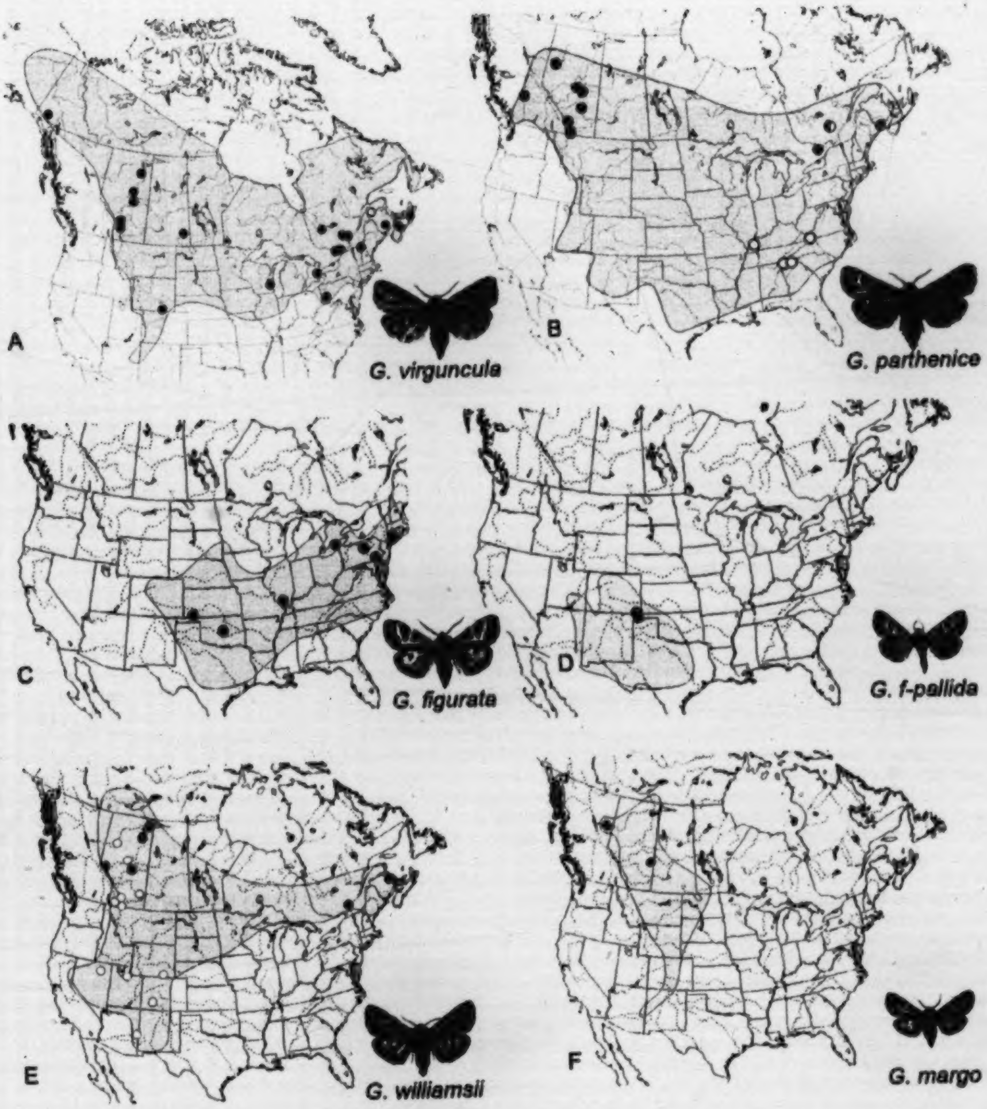

A
G. virguncula
B
G. parthenice
C
G. figurata
D
G. f-pallida
E
G. williamsii
F
G. margo

Figure 3-4a-f. Approximate geographic ranges of species (shaded) exhibiting Eastern lineage haplotypes. Solid circles represent sampling localities of individuals with Eastern lineage haplotypes, white circles non-Eastern lineage haplotypes, and half-filled circles both Eastern and non-Eastern haplotypes.

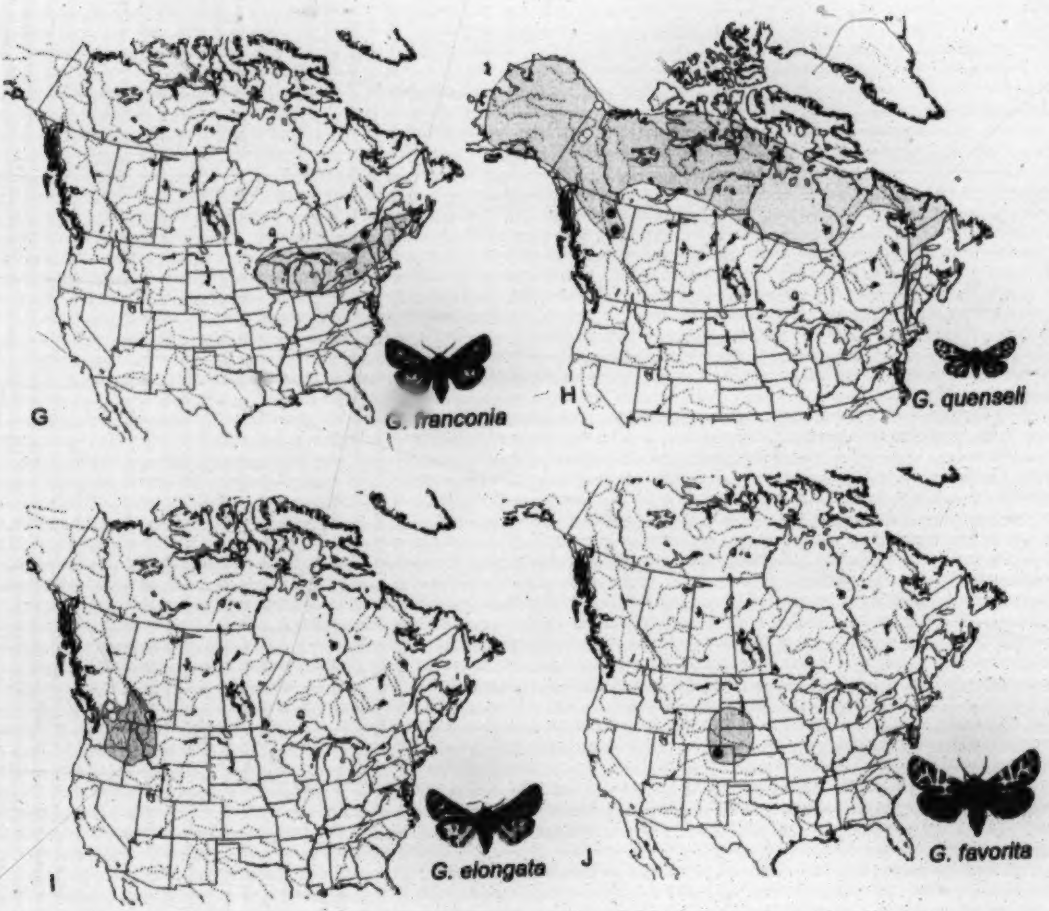

G
G. franconia
H
G. quenseli
I
G. elongata
J
G. favorita

Figure 3-4i-j. Approximate geographic ranges of species (shaded) exhibiting Eastern lineage haplotypes. Solid circles represent sampling localities of individuals with Eastern lineage haplotypes, white circles non-Eastern lineage haplotypes, and half-filled circles both Eastern and non-Eastern haplotypes.

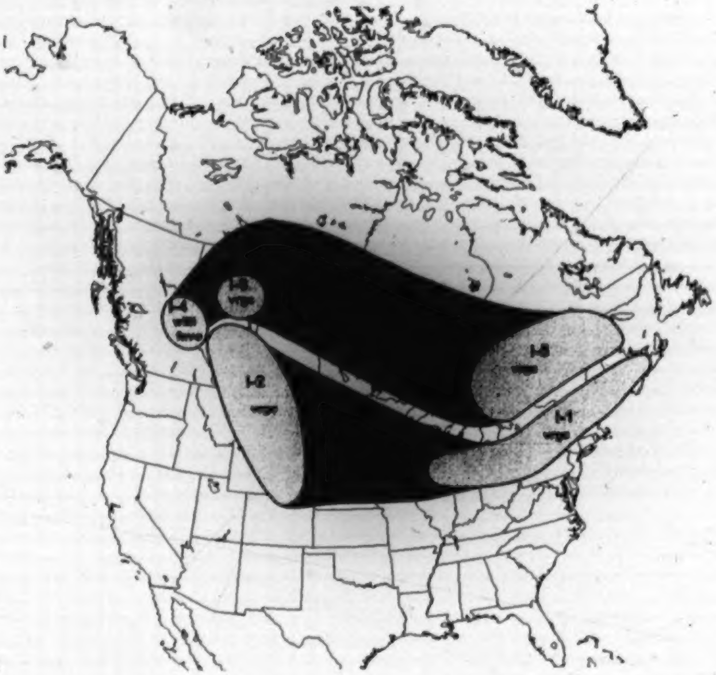


Figure 3-5a. Approximate geographic overlay of sampling localities (Figure 3-4) and haplotypes according to nesting clades shown in Figure 3-3, for clade III-1. Orange indicates haplotypes of 1-step clades, blue indicates 2-step clades. Species represented by each one-step clade are abbreviated as follows: vrgc - *G. virguncula*; willi – *G. williamsii*; favo – *G. favorita*.

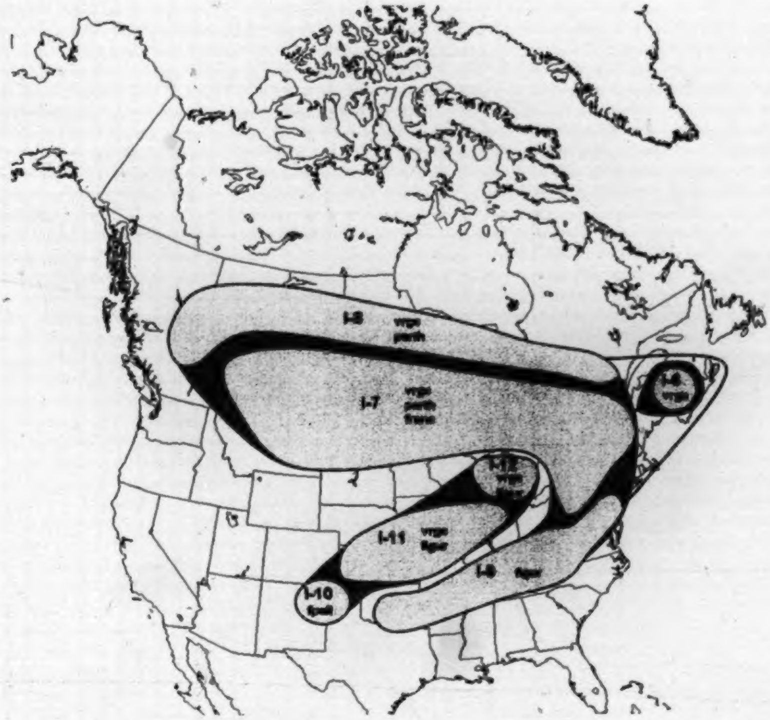

I-5
vrgc
parth
I-7
vrgc
parth
franc
I-6
vrgc
I-12
vrgc
I-11
vrgc
figur
I-8
figur
I-10
fpall

Figure 3-5b. Approximate geographic overlay of sampling localities (Figure 3-4) and haplotypes according to nesting clades shown in Figure 3-3 for clade III-2. Orange indicates haplotypes of 1-step clades, blue indicates 2-step clades. Species represented by each one-step clade are abbreviated as follows: vrgc - *G. virguncula*; parth – *G. parthenice*; franc – G. franconia; figur – *G. figurata*; fpall – *G. f-pallida*.

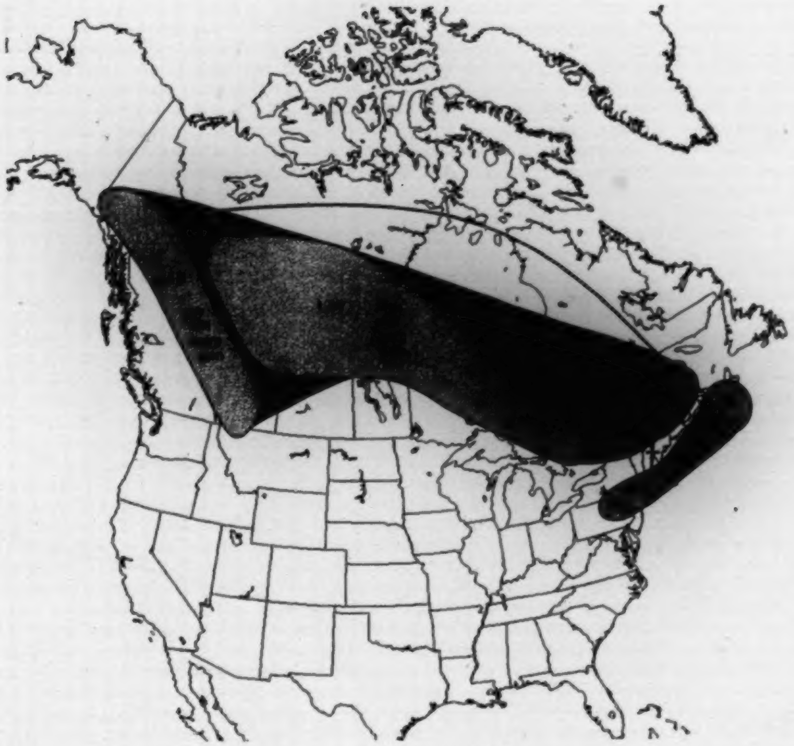


Figure 3-5c. Approximate geographic overlay of sampling localities (Figure 3-4) and haplotypes according to nesting clades shown in Figure 3-3 for clade [III-3 + III-4]. Orange indicates haplotypes of 1-step clades, blue indicates 2-step clades. Species represented by each one-step clade are abbreviated as follows: vrgc - *G. virguncula*; willi – *G. williamsii*; figur – *G. figurata*; marg – *G. margo*; elon – *G. elongata*; quen – *G. quenseli*.

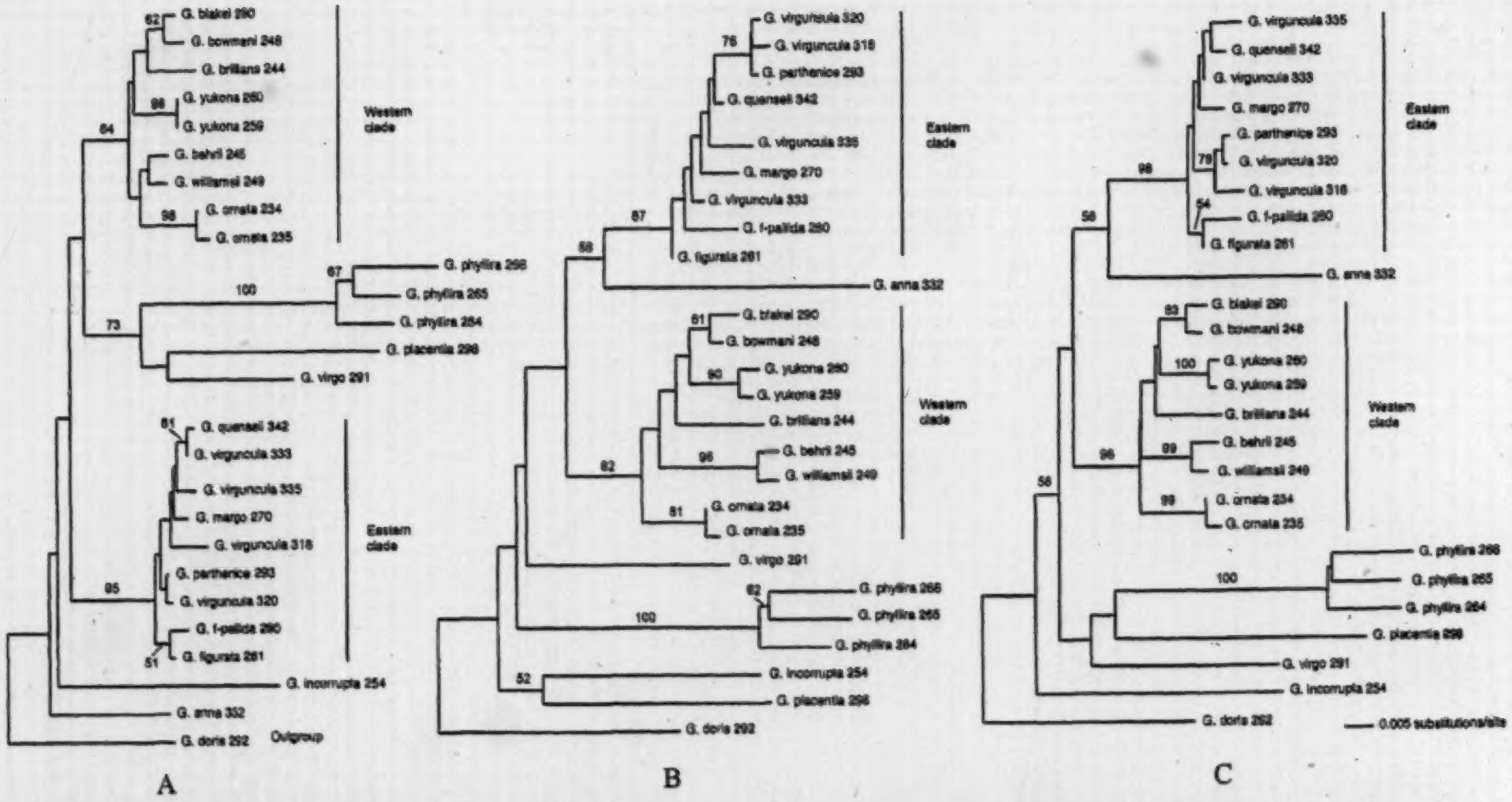

62
G. blakei 290
G. bowmani 248
G. brillians 244
98
G. yukona 260
G. yukona 259
Western clade
84
G. behrii 245
G. williamsi 249
98
G. ornata 234
G. ornata 235
67
G. phyllira 266
100
G. phyllira 265
73
G. phyllira 264
G. placentia 298
G. virgo 291
81
G. quenseli 342
G. virguncula 333
G. virguncula 335
G. margo 270
Eastern clade
G. virguncula 318
G. parthenice 293
95
G. virguncula 320
G. f-pallida 280
51
G. figurata 281
G. incorrupta 254
G. anna 332
G. doris 292
Outgroup
A
G. virguncula 320
76
G. virguncula 318
G. parthenice 293
G. quenseli 342
G. virguncula 335
Eastern clade
G. margo 270
G. virguncula 333
87
G. f-pallida 280
88
G. figurata 281
G. anna 332
61
G. blakei 290
G. bowmani 248
90
G. yukona 260
G. yukona 259
G. brillians 244
Western clade
96
G. behrii 245
82
G. williamsi 249
81
G. ornata 234
G. ornata 235
G. virgo 291
62
G. phyllira 266
100
G. phyllira 265
G. phyllira 264
52
G. incorrupta 254
G. placentia 298
G. doris 292
B
G. virguncula 335
G. quenseli 342
G. virguncula 333
G. margo 270
Eastern clade
G. parthenice 293
79
G. virguncula 320
98
G. virguncula 318
54
56
G. f-pallida 280
G. figurata 281
G. anna 332
93
G. blakei 290
G. bowmani 248
100
G. yukona 260
G. yukona 259
G. brillians 244
Western clade
96
99
G. behrii 245
G. williamsi 249
56
99
G. ornata 234
G. ornata 235
G. phyllira 266
100
G. phyllira 265
G. phyllira 264
G. placentia 298
G. virgo 291
G. incorrupta 254
G. doris 292
0.005 substitutions/site
C

Figure 3-6. Comparison of phylograms for 26 specimens of 19 *Grammia* species based on the Barcode, Jerry-Pat and combined Barcode / Jerry-Pat fragments of *cox1*. **a)** one of 31 most-parsimonious phylograms for the Barcode fragment, **b)** one of 16 most parsimonious phylograms for the Jerry-Pat fragment, and **c)** one of nine most parsimonious phylograms for the combined Barcode and Jerry-Pat fragments. Numbers at nodes indicate bootstrap support values greater than 50%. Sample numbers correspond to 'BCSC___' numbers in Appendix 2-1.

Chapter 4.

Phylogeny and classification of the *Neoarctia-Grammia* group of genera (Lepidoptera: Noctuidae: Arctiinae: Arctiini)

INTRODUCTION

Among the Lepidoptera, tiger moths (Arctiinae[1]) are known for a variety of unique evolutionary attributes, most notably for their ability to produce toxins from both toxic and non-toxic food plants (Weller et al. 1999 provide a review), and the ability to emit ultrasound audible to bats (Fullard and Fenton 1977). Believed to have initially evolved as predator defense mechanisms, toxin and sound production function as courtship cues in several arctiine lineages (Weller et al. 1999).

Although a phylogenetic framework for the Arctiinae would provide insights into the evolution of the complex chemical and acoustic ecology of tiger moths, a comprehensive phylogenetic analysis of the Arctiinae has only recently been attempted (Jacobson and Weller 2002), which confirmed the monophyly of the group (Holloway 1988, Kitching and Rawlins 1998), and resolved the main tribal relationships. Three tribes are recognized within the Arctiinae, namely Lithosiini, Syntomini, and Arctiini, corresponding to the subfamilies of Kitching and Rawlins (1998), with the Lithosiini + Syntomini believed to be the sister group of the Arctiini (Fig. 4-1). The Arctiini contain approximately 4,400 of the world's 11,000 arctiine species (Kitching and Rawlins 1998). The phylogeny of major lineages within the Arctiini are partially resolved, in that the subtribes Callimorphina, Pericopina, Phaegopterina, Ctenuchina and Euchromiina form relatively well-supported clades (Fig. 4-1; Jacobson and Weller 2002). Phylogeny of the Cteunchina and Euchromiina remains problematic (Simmons and Weller 2001).

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[1] Family-group names of the Noctuoidea have recently been revised to reflect changes in the phylogeny of the group (Lafontaine and Fibiger 2006), with the Arctiidae now recognized as a subfamily of the Noctuidae, and previously delineated subfamilies equal to tribes, and tribes as subtribes. This new nomenclature is followed throughout this chapter.

Taxonomic History

The genera related to *Arctia* Schrank, *Grammia* Rambur, and *Spilosoma* Curtis have been grouped together based on larval morphology and gross genitalic structure, and included as such in the Arctiina (= Arctiini, e.g. Forbes 1939, 1960; Ferguson 1985; de Freina and Witt 1987; Bendib 2003). The Arctiina *sensu lato* contains approximately 113 genera and has a global distribution, with the highest diversity in temperate and tropical Asia (Kôda 1987, 1988; Holloway 1988).

Spilosoma and related genera also have a global distribution, but are especially rich (at both the species and genus level) in Asia (Kôda 1987, 1988; Holloway 1988). In contrast, the *Arctia* and *Grammia* generic group occur almost exclusively in the Holarctic region, with the highest diversity in temperate Asia. The species and genera related to (and including) *Arctia* and *Grammia* are among the few lepidopteran species that inhabit the high arctic, with the *Neoarctia-Grammia* group (Ferguson 1985) forming a subset of those that are the focus of this study. The high proportion of genera with arctic and holarctic distributions makes this group particularly interesting from a biogeographical perspective, and the systematic position of *Grammia*, the largest North American genus, remains unresolved. Furthermore, the subgenera within *Grammia* as previously defined are distantly related, and the genus is not monophyletic.

There have been no directed attempts at resolving the phylogeny of the Arctiina (*s.l.*). Earlier authors such as Hübner (1816) and Kirby (1892) based groupings within the Arctiinae largely on superficial appearance, and generally did not differentiate groupings within Arctiina, or in some cases within Arctiini. DaCosta and Weller (2005) provide an extensive literature review of the historical classification of the Arctiini. Bendib and Minet (1998) suggested possible synapomorphies of Arctiini subtribes based primarily on female pheromone gland morphology (Fig. 4-2), but the relationships suggested therein differ substantially from subsequent work (Fig. 4-1).

Forbes (1939, 1960) was apparently the first author to define groups within the Arctiina based on morphological characters. He united the North American genera of the group into the Arctiina based primarily on larval and pupal characters, in addition to three adult characters. Forbes included *Grammia* (as *Apantesis* Walker, in part) in his group "C", defined by a pale forewing pattern on a dark background, and the dorsal edge of the male valve base articulating above the juxta (Forbes 1960). This group also included *Arctia* and related genera, i.e. Arctiina *s.s.* (Fig. 4-3).

Ferguson (1985), expanding on the characters of Forbes (1939, 1960), united the Arctiina based on the following traits: 1) forewing pattern, 2) male valve, juxta and uncus simple, 3) larvae without hair pencils, 4) larvae polyphagous on herbaceous plants, 5) pupal abdominal segments 5-7 preceded by furrow, with movable segments, 6) anterior margin of pupal segments 5-7 with a flange directed posterad, 7) pupal wing cases touching midventrally, and 8) pupal maxillae not extending beyond point where wings meet. As discussed by Jacobson and Weller (2002), some of these characters (3,5) appear to be plesiomorphic, and character 6 can be sexually dimorphic in some genera (e.g. *Hyphantria*). The specific pale-on-dark forewing pattern considered by Ferguson to be unique to Arctiina occurs also in the genus *Cymbalophora* Rambur of the Callimorphina. Characters 4, 7, and 8 are potential apomorphies. Bendib and Minet (1998) suggested that a branched female dorsal pheromone gland could be a synapomorphy of the Arctiina.

Ferguson (1985) recognized five genus-groups globally within the Arctiina (Fig. 4-3), based in part on the groups recognized by Forbes (1960). Ferguson (1985) provided only a cursory treatment of the enormous *Spilosoma* group, the most diverse in the Arctiina *sensu lato*. Kôda (1987, 1988) reviewed the Palaearctic and Oriental genera of Arctiini, recognizing six genus groups, partially corresponding to Ferguson's (1985) Arctiina groups (Fig. 4-3) in addition to the Callimorphina and Phaegopterina (*sensu* DaCosta and Weller 2005). Kôda (1987, 1988) did not include taxa extralimital to the Oriental region. Dubatolov (1996) recognized three Arctiina *s.l.* subtribes, splitting the Arctiina into the Arctiina *s.s.*, Micrarctiina, and Spilosomina (Fig. 4-3). Although possible synapomorphies were proposed by Ferguson (1985) and Kôda (1987, 1988) for each genus group, no relationships among groups were proposed by these authors. Bendib and Minet (1998) proposed that (*Neoarctia* + *Grammia*) and (*Diacrisia* + *Rhyparioides* + *Rhyparia*) may be sister groups (Fig. 4-2), although Ferguson placed the latter three genera in his *Spilosoma* group (Fig. 4-3). Bendib and Minet (1998) also speculated on the monophyly of a group consisting of (*Virbia* + [*Arctia* + *Hyphoraia*] + [*Phragmatobia* + *Ocnogyna* + *Spilosoma*]) (Fig. 4-2).

Ferguson (1985) placed *Grammia* as part of the *Neoarctia-Grammia* group, consisting of the following genera: *Holoarctia* Ferguson, *Neoarctia* Neumögen and Dyar, *Holarctia* M.E. Smith[2], *Hyperborea* Grum-Grshimailo, *Chelis* Rambur, *Grammia*, *Notarctia* M.E. Smith, and *Apantesis*. He considered *Grammia* to be most closely related to *Apantesis* and *Notarctia*, based on a shared forewing venation character, namely R2 and R3 arising separately from the discal cell. Ferguson considered (*Notarctia* + *Apantesis*) to be the sister group of *Grammia* (Ferguson 1985: 233). The characters used by Ferguson to define this group include presence of transverse and/or longitudinal pale bands on the forewing, forewing accessory cell usually absent, and foretibial claws absent; male genitalia with transtilla absent or rudimentary, gnathos absent; distribution limited to northern hemisphere. The only definitive apomorphy for this group appears to be certain elements of the longitudinal forewing pattern expressed in some genera (Ferguson 1985: 187-188).

Kôda (1987) included *Grammia* in the *Rhyparioides* group, consisting of *Grammia, Chelis,* and *Neoarctia* (based on a specimen misidentified as *Hyperborea czekanowskii* Grum-Grshimailo), which was in this respect similar to Ferguson's *Neoarctia-Grammia* group. Kôda also included *Diacrisia* Hübner, *Rhyparia* Hübner, and *Rhyparioides* Butler, genera which Ferguson thought more closely related to *Spilosoma*. Kôda proposed two synapomorphies for the *Rhyparioides* group: the flattened, concave male valve apex, and the sclerotized invagination of the female lamella postvaginalis.

Dubatolov (1996) treated Ferguson's *Neoarctia-Grammia* and Kôda's *Rhyparioides* group genera as the Micrarctiina, which also included *Divarctia* Dubatolov, *Tancrea* Püngeler, *Centrarctia* Dubatolov, *Micrarctia* Seitz, *Amurhyparia* Dubatolov, *Sibirarctia* Dubatolov and *Virbia* Walker (=*Holomelina* Herrich-Schäffer). Ferguson either did not consider these genera, or placed them in other genus-groups (Fig. 4-3). Kôda examined two species included in *Micrarctia* at that time, *M. y-albulum* (Oberthür) and *M. kindermanni* (Staudinger), both of which he included in the *Spilarctia* group. *Y-*

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[2] included by Ferguson (1985) as *Palearctia* Ferguson; note distinction between *Holoarctia* Ferguson and *Holarctia* M.E. Smith.

albulum and *kindermanni* were subsequently transferred to *Lithosarctia* and *Sibirarctia*, respectively (Dubatolov 1987, 1996), leaving the enigmatic genus *Micrarctia* monotypic. Dubatolov (1996) included *Sibirarctia* in the Micrarctiina, and retained *Lithosarctia* in the Spilosomina.

Using a 537 base-pair fragment of 16s rDNA, Wink and Nickisch-von Rosenegk (1997) found the Arctiina to be non-monophyletic with respect to *Callimorpha* Latreille (type genus of the Callimorphina), although only four Arctiina genera were sampled and no other character systems were examined (methodology subsequently questioned by Brower [1998]). Jacobson and Weller (2002) included seven Arctiina genera among the 39 representing all Arctiini subtribes, and Arctiina was not recovered as monophyletic, based on 65 morphological characters, largely those of larvae. Although *Grammia* was not included in that analysis, *Apantesis* consistently placed as the sister group to *Spilosoma* of the seven Arctiina genera included therein (Fig. 4-1). The tribal relationships within Arctiinae tentatively proposed by Bendib and Minet (1998) differed substantially from those of Jacobson and Weller (2002), but the composition of the Arctiina essentially followed that of Ferguson (1985) (Fig. 4-2).

In summary, there is little consensus of group membership within Arctiina *s.l.*, and no comprehensive phylogeny for these groups has been proposed. The genera included appear to represent a paraphyletic assemblage (Jacobson and Weller 2002, DaCosta and Weller 2005; Fig 4-1).The purpose of this chapter is to place *Grammia* into a phylogenetic context, and to provide a preliminary phylogeny of the Arctiina using morphological and molecular data. The morphological characters used here build on those previously used in assessing arctiine phylogenies, in addition to a number of novel character systems that appear to be valuable for determining relationships within the Arctiina. Several synapomorphies are proposed for clades previously treated as the Arctiina *s.l.*

METHODS AND MATERIALS

Taxon sampling

Taxon sampling was comprehensive for all genus groups proposed by Ferguson (1985) (Table 4-1, Fig. 4-3), including 13 of the 25 genera included in the *Arctia-Hyphoraia* and *Neoarctia-Grammia* groups. Three of the four groups within Arctiina (*s.l.*) proposed by Kôda (1987, 1988) were also represented by at least two genera (Fig. 4-3). Based upon previous subtribal or genus groups, I selected 24 representative ingroup genera, and five internal outgroup genera representative of the remaining Arctiini subtribes (Table 4-1). Of the 24 ingroup taxa used in the morphology analysis, five were not used in the molecular and combined analyses due to lack of data: *Chelis, Leptarctia, Ocnogyna, Rhyparia* and *Rhyparioides*.

Two *Grammia* species representing the two subgenera were selected (Chapter 2). Subgenus *Mimarctia* Neumögen and Dyar contains two species, while subgenus *Grammia* contains the remaining 34 named *Grammia* species, but there is very little variation in genitalic morphology within the subgenus (Chapter 2), and species sampling was therefore limited to one representative species, *Grammia virgo* (L.). Two lithosiine genera were selected as external outgroups, since the Lithosiini + Syntomini are well-supported as a sister group to the Arctiini (Jacobson and Weller 2002). Internal outgroup genera included at least one genus from each Arctiini subtribe outside of the Arctiina (Table 4-1), with the exception of the Euchromiina (see below).

Excluded taxa

Syntomeida was initially included as a representative of the Euchromiina, but proved to be so morphologically divergent as to render it difficult to determine possible homologies for many genitalic characters, and was therefore not included in the analysis. Fifteen of the 34 world genera of Arctiina + Micrarctiina (*sensu* Dubatolov 1996), in addition to seven Spilosomina genera were included for morphological analysis. The genera *Rhyparia, Rhyparioides, Ocnogyna* and *Leptarctia* were not available for mtDNA analysis (Table 4-1).

The genus *Kodiosoma* Stretch has consistently been placed in the Arctiina *s.l.* (Franclemont 1983, Ferguson and Opler 2006), and Ferguson (1985) included it within the *Phragmatobia-Ocnogyna* group. Examination of the male genitalia of *Kodiosoma fulva* Stretch shows this genus to be allied to *Cycnia* and *Euchaetes* of the Phaegopterina, as first suggested by Dubatolov (2003). The uncus base is broadly lobed, the dorsal tegumen displays dense hair brushes, and the external valve has a membranous lobe, much like the *Cycnia-Euchaetes* group (DaCosta and Weller 2005). These characters are derived within the Arctiini, and do not occur elsewhere in the Arctiina *sensu lato*. *Kodiosoma* was therefore not included for further analysis.

Franclemont (1983) included *Dodia* in the Arctiina, but Ferguson (1985) believed it to be a callimorphine, where it is now placed (Dubatolov 1996, 2006; Ferguson and Opler 2006). Dubatolov (2006) placed *Dodia* as the sister genus to *Tyria* (Callimorphini) based on genitalic morphology, a relationship supported by *cox1* sequence data (BCS, unpubl. data). Although the genus was omitted from a global phylogeny and checklist of the Callimorphini (DaCosta and Weller 2005), it is almost certainly a callimorphine and not an arctiine, and is therefore not considered further here.

Sampling of non-molecular characters

Eighty-one characters were established, 52 based on male genitalic structure, and 28 based on non-genitalic morphology. Diapause stage was also included as a character, as it was deemed important in Arctiina group membership by Ferguson (1985). Sixty-six characters were coded as binary, and 15 as multi-state. Twenty-four characters were based on those previously used in arctiid phylogenies (Jacobson and Weller 2002, DaCosta and Weller 2005). The remaining characters have either not previously been used in arctiid phylogenetic analyses (but used to define genus-groups within the Arctiini *s.l.*), or were novel characters established herein. All characters were treated as unordered, with the exception of character 50 (Appendix 1). For character 50, three states, each with a weight of 1, were assigned: transtillar process absent (0), present, unarmed (1), and present, scobinate (2). This character was treated as ordered since it is reasonable to assume that the transtillar process must be present to exhibit modifications such as scobinations.

A high proportion of the characters used by DaCosta and Weller (2005) were constant among the taxa examined here, and were therefore not included. Female characters were not included because female specimens of all sample genera were not available. Wing pattern was used as a character to define genus-groups by Ferguson (1985), but wing pattern elements proved difficult or impossible to score across all outgroups since homologies are not obvious among highly varied color patterns. Wing pattern was therefore not included as a character system.

Morphological techniques

Adult genitalia were prepared following the methods detailed by Lafontaine (2004). Whole-body preparations were examined and stored temporarily in 70% ethanol, and genitalia and abdominal pelts were subsequently mounted in Canada Balsam. Thoraces and head capsules were stored in glycerol. Wing venation was examined by wetting the wings with xylene. Genitalic terminology follows Klots (1970). To illustrate characters and states, pencil drawings were made using a camera lucida, and subsequently inked by hand.

Molecular techniques

Molecular variation was assessed based on the 658 base-pair (bp) barcode region of the cytochrome oxidase I (*cox1*) gene of the mitochondrial DNA genome (Hebert et al. 2003). Number of sequenced specimens per species depended on availability, and varied from one (*Diacrisia sannio, Arachnis picta*) to 25 (*G. virgo*). For species with multiple sequences, one sequence was chosen arbitrarily for analysis, after screening for spurios sequence through neighbour-joining analysis of conspecific sequences. One or two legs of dried, fresh frozen or ethanol-preserved specimens were sent to the University of Guelph in dry Eppendorf tubes, and processed as part of the "All Leps Barcode of Life Campaign" (www.lepbarcoding.org). DNA extraction, amplification and sequencing protocols for the Barcode of Life initiative are detailed in Hebert et al. (2003).

Phylogenetic analysis

Phylogenies using the morphological, *cox1* and combined data sets were estimated using maximum parsimony (MP) phylogenetic analysis implemented in PAUP 4.0*b10 (Altivec) (Swofford 2002), using heuristic searches with the following parameters: 100 random addition replicates; stepwise addition; tree bisection-reconnection (TBR). Branch support was calculated using bootstrap support values, obtained through 100 bootstrap replicates using the heuristic search methods given above. Character states for internal nodes were assigned using accelerated transformation (ACCTRAN) optimization in PAUP. The lithosiines *Eilema bicolor* (Grote) and *Hypoprepia miniata* (Kirby) were selected as a monophyletic outgroup in all analyses.

RESULTS

Clade membership and bootstrap support for clades differed depending on the phylogenetic dataset, particualrly with respect to placement of *Virbia*. in the Mr and MR+*cox1* data, *Virbia* places outside of the Arctiina (Figs. 4-4, 4-6). The *cox1* data, however, places *Virbia* nested within the Arctiina-clade as sister to *Notarctia* (Fig. 4-5). HOwever, only the clades *Holoarctai+Neoarctia, Platarctia+Pararctia,* and *Phragmatobia+Pyrrharctia* have 80% bootstrap support or greater. Some discrepancies in topologies using differing character systems, particularly among morphological and molecular datasets, are to be expected, since the number of characters of each data type differ substantially and represent fundamentally different evolutionary histories. Analysis of combined molecular and non-molecular data has however proven to be more phylogenetically informative than the sum of separate analyses (see e.g. Wahlberg et al. 2005).

Maximum parsimony analysis of the morphology (MR) dataset of 81 characters resulted in 31 most parsimonious trees, the consensus of which was highly resolved (Fig. 4-4). Thirteen of the 81 characters were parsimony uninformative, but are included here for future reference, particularly for comparison of additional arctiine genera. Analysis of the *cox1* dataset resulted in 37 most parsimonious trees (tree length: 1134; Fig. 4-5), with

269 (of 658) variable sites, 173 of which were parsimony informative. The *cox1* consensus tree was moderately resolved (Fig . 4-5). The combined dataset (MR+*cox1*) yielded three most parsimonious trees, the consensus of which is shown in Fig. 4-6.

The topology of the *cox1* dataset showed all 19 ingroup genera to be monophyletic (Clade F, Fig. 4-5). With the exception of *Virbia*, the ingroup genera were also monophyletic in the MR (Fig 4-4) and MR+*cox1* (Fig. 4-6) analyses; *Virbia* placed with internal outgroup genera in the MR (Clade G, Fig. 4-4) and MR+*cox1* (Fig. 4-6) datasets. The *cox1* analysis did not recover the external outgroup genera as monophyletic (Fig. 4-5). Although resolution of the ingroup topology was limited in the *cox1* dataset, resolved nodes were largely congruent with the MR tree topology. Based on the MR tree topology, the ingroup genera are monophyletic (Clade F, Fig. 4-4, 4-5, 4-6), with seven morphological synapomorphies, none unique to the clade (Table 4-2). With the exception of *Virbia*, this clade corresponds to the Arctiina *s.l.*

Clade E, consisting of *Pyrrharctia, Estigmene, Arachnis, Phragmatobia, Leptarctia, Ocnogyna* and *Spilosoma*, had a bootstrap support of 65%, with 12 synapomorphies, two of which were not shared by any other taxa examined (Table 4-2). The same clade was recovered in the *cox1* dataset with no bootstrap support (Fig. 4-5), and in the combined dataset with a bootstrap support of 54% (Fig. 4-6). The *Phragmatobia-Ocnogyna* group (Ferguson 1985) nested within clade E, and the *Spilosoma* group is paraphyletic with five genera in clade E and three in clade D (Fig. 4-4).

Clade D formed a sister group to Clade E (Figs. 4-4, 4-6), and consisted primarily of Arctiina *s.l.* genera not included in the *Spilosoma* and groups (Ferguson 1985). *Diacrisia, Rhyparia*, and *Rhyparioides* (*Spilosoma* group, *sensu* Ferguson 1985) were part of this clade. Clade D is supported by six MR synapomorphies, none of which were unique to the clade (Table 4-2).

Clades A, B and C were subclades of Clade D. Representative genera of the *Arctia* (Kôda 1987) / *Arctia-Hyphoraia* (Ferguson 1985) group were consistently monophyletic, forming Clade A (Fig. 4-4), and supported by three MR synapomorphies, one of which was unique to this clade (Table 4-2). Both *Grammia* subgenera (*Mimarctia* and *Grammia*) plus *Apantesis* and *Notarctia* formed clade B (Fig. 4-4). *Holarctia*, previously treated as a subgenus of *Grammia* (Chapter 2), was paraphyletic with respect to clade B in the MR dataset; however, the *cox1* and MR+*cox1* datasets recovered Clade B + *Holarctia* as monophyletic, with low bootstrap support (61%) in the latter (Figs. 4-5, 4-6). The MR tree topology resulted in five synapomorphies for clade B, none unique to the clade (Table 4-2). *Grammia* was monophyletic only in the MR analysis (Fig. 4-4).

Clade C, consisting of *Neoarctia, Holoarctia* and *Chelis*, showed low bootstrap support (57%) for the MR dataset, with high bootstrap support for *Neoarctia* + *Holoarctia* in the *cox1* (86%) and MR+*cox1* (98%) analyses (mtDNA sequence data was not available for *Chelis*). This clade was supported by seven MR synapomorphies, one of which (character 42) was unique to this clade (Table 4-2).

Interpretation of the scaphium in *Virbia*

The presence of a scaphium (character 47: 1) in male *Virbia* (Zaspel and Weller 2006; gnathos of Ferguson 1985) is highly unusual for any Arctiinae, and if correctly interpreted may be unique within the subfamily. It should be noted however that the scaphium could be the apex of the uncus, and the uncus apex is really a process developed dorsocaudally from the base of the uncus, as seen in *Pericallia* Hübner (Arctiina *s.s.*; illustrated in Kôda 1987: 210, fig. 34a) and *Eucharia* Hübner (Arctiina *s.s.*; illustrated in Kôda 1987: 195, fig. 25a). Although these genera are superficially quite different from *Virbia* (and restricted to the Palaearctic, while *Virbia* is entirely Nearctic/Neotropical), a re-interpretation of the *Virbia* scaphium as a modified uncus is more parsimonious with the placement of *Virbia* in the Arctiina based on *cox1* data (Fig. 4-5) and larval characters (Forbes 1939, Jacobson and Weller 2002).

DISCUSSION

Arctiina *sensu lato* (Clade F)

Nearly all genera examined here that have been placed in the subtribe Arctiina (*sensu* Forbes 1939, 1960; Ferguson 1985; de Freina and Witt 1987; Bendib 2003), formed a monophyletic group in all most-parsimonious trees for both data partitions and the combined data set (Clade F; Figs. 4-4, 4-5, 4-6). A notable exception to the monophyly of the Arctiina *s.l.* was the placement of *Virbia*, discussed below. There were no unique morphological synapomorphies for this clade, and synapomorphies consisted of vein R2 and R3 of forewing connate or stalked (18:1), antecosta of sternite A8 present (26: 1), dorsal tegumen not expanded proximally into rounded areas (32: 0), manica reinforced (53: 1), dorsum of juxta straight or slightly rounded (55:1), distal opening of aedeagus without caudal component (73: 0), and aedeagus long (76: 0). Consistency indices for these characters were low, however (Table 4-2), and bootstrap support was less than 50% for this clade in all three analyses (Figs. 4-4, 4-5, 4-6).

The character sets employed by Jacobson and Weller (2002) did not resolve the Arctiina *s.l.* as monophyletic, with both *Paracles* and *Apantesis+Spilosoma* paraphyletic with respect to (*Phragmatobia, Pyrrarctia, Virbia, Platyprepia*) (Fig. 4-1, 4-3). Five synapomorphies supported the latter clade, (Jacobson and Weller 2002), none of which were unique. Exemplar taxa used herein were congeneric with (*Virbia, Apantesis*), or identical to those used by Jacobson and Weller in their study, although *Paracles* was unavailable, and not included here. There is little agreement between the topologies of these genera as resolved here compared to that of Jacobson and Weller (2002); however, given the difference in focus on taxonomic level (tribes vs. genus-groups), incongruence between these two topologies is not surprising.

Neoarctia-Grammia group

Bendib (2003) synonymized *Holoarctia* under *Grammia*, without additional comment. Ferguson (1984, 1985) summarized the numerous morphological differences between *Grammia* and *Holoarctia*, and did not consider these genera as sister groups, a view supported by the data presented herein (Figs. 4-4, 4-5, 4-6). *Holoarctia* and *Grammia* are therefore retained as separate genera.

The six genera of the *Neoarctia-Grammia* group were not monophyletic in analyses of either the individual or combined data sets, although there was high bootstrap support (86% and 98%) for a clade consisting of *Holoarctia* + *Neoarctia* (Clade C, Figs. 4-5, 4-6), with low support (57%) for the MR dataset consisting of *Holoarctia* + *Neoarctia* + *Chelis* (Fig. 4-4). This clade was supported by seven synapomorphies (Table

4.2), one of which was unique: the uncus is sinuate in lateral view (42: 1; Fig. 4-8b). *Grammia, Notarctia* and *Apantesis* grouped together, with low bootstrap support (54%) for this clade in the MR+*cox1* dataset (Clade B, Fig. 4-6); *Holarctia obliterata* was not part of this clade in the analysis based on the MR data (Fig. 4-4).

Arctia-Hyphoraia group (Clade A)

Kôda (1987) suggested the presence of a pedunculus, here termed transtillar process (character 50), as an synapomorphy for the *Arctia* group. In addition to the genera examined by Kôda, this process occurs in *Parasemia, Platarctia, Pararctia* and *Platyprepia* (50: 1,2), forming clade A (Figs. 4-4, 4-5, 4-6). The transtillar process also occurs in *Borearctia* (Dubatolov 1984), *Acerbia*, and *Hyphoraia* (Sotavalta 1965). Two additional synapomorphies support clade A, a well-developed transtilla (49: 1) and an elongate, cylindrical valve apex (60: 2). This clade, treated by Dubatolov as the Arctiina and largely corresponding to Ferguson's *Arctia-Hyphoraia* group (Fig. 4-3), is tentatively supported as monophyletic.

Spilosomina

Ferguson (1985) differentiated the *Phragmatobia-Ocnogyna* (PO) group from the *Spilosoma* (SP) group based on wing colour and pattern, presence of the forewing accessory cell, characters of the male genitalia, geographic distribution, and diapause stage. None of these characters are definitive apomorphies, since character states are shared with other Arctiina *s.l.* genera, and are often variable within the genus-group, genus or even species. For example, Smith (1938) showed that the presence of the accessory cell can vary within species of *Grammia*.

The PO and SP group genera were not reciprocally monophyletic in the *cox1*, morphology or combined data sets (Figs. 4-4, 4-5, 4-6). Indeed, the *cox1* phylogeny shows high bootstrap support (92%) for *Phragmatobia* (PO group) and *Pyrrharctia* (SP group) as sister genera (Fig. 4-5). Although only the MR+*cox1* dataset exhibited bootstrap values greater than 50% for a PO+SP clade (clade E, Fig 4-6), this clade was recovered in all most-parsimonious trees for all datasets (Figs. 4-4, 4-5, 4-6). Two unique synapomorphies support the PO+SP clade taxa examined here: a ridge-like, dorsally or caudodorsally directed anterior portion of the dorsal tegumen (31: 1; Fig. 4-8a), and the presence of lateral sclerites or lobes on the 8th abdominal sternite of the male (29: 1; Fig. 4-8a). The latter is membranous and difficult to see in some genera such as *Phragmatobia*, but is present as a membranous out-pocket positionally homologous with the apex of the lateral sclerite in taxa where it is strongly developed (e.g. *Seirarctia* Packard, *Pyrrharctia*). The lateral sclerite is also present in all genera included by Kôda in the *Spilarctia* group (Kôda 1988), as is the ridge-like dorsum of the tegumen. In addition to the genera examined by Kôda (1988), the A8 lateral sclerite is present in the Asian genera *Lemyra* Walker, *Areas* Walker, and *Aethalidia* Walker (Holloway 1988). Ten additional synapomorphies supported clade E, listed in Table 4-2. An elongate tarsal 'flap' (14: 1; Fig. 4-7a) was also unique to this clade, although a reversal to the 'broad' condition (Fig. 4-8b) occurs in *Phragmatobia, Leptarctia and Ocnogyna.* Pheromone constituents of the Spilosomina may represent another synapomorphy of this group. Millar (2000) noted that only seven Arctiinae species are known to produce 18-carbon female pheromone compounds (Z,Z-9,12 octadecadienal and/or Z,Z,Z-9,12,15 octadecatrienal), namely *Estigmene acrea*, *Phragmatobia fuliginosa* (L.), *Spilosoma lubricipedum* (L.), *Hyphantria cunea* (Drury), *Spilarctia obliqua* (Walker), *Spilarctia lutea* (Hufnagel), and *Amsacta albistriga* (Walker). The phylogenetic affinities of Estigmene, Phragmatobia and Spilosoma have already been dealt with herein; *Hyphantria* is a North American genus related to *Spilosoma* (Schmidt, unpubl. data), and *Spilarctia* and *Amsacta* were treated as part of the *Spilarctia* group by Kôda (1988). The monophyly of the Spilosomina therfore appears to be well-supported.

Several other genera currently placed in the PO group require comment. *Sonorarctia* Ferguson 1985 occurs from southern Arizona to Guatemala, and currently includes two species, *nundar* (Dyar) and *fervida* (Walker). Ferguson (1985) placed this genus in the PO group based on the presence of a well-developed transtilla (48: 1), a broad uncus (43: 1; Fig. 4-8e), and a lateral lobe on the vinculum (34: 1). These characters are not unique to this group (clade E), although a simple, well-developed vincular lobe occurs only in some clade E genera. More importantly, the ridged dorsal tegumen and lateral lobe does not occur in *Sonorarctia* (Ferguson 1985), and the forewing pattern is very similar to *Apantesis* and unlike anything in the Spilosomina (as defined here). Furthermore, the juxta is scobinate and the dorsal part of the male valve is flattened, both characters of the Arctiina *s.s.* (clade D, Table 4-2). Ferguson also remarked on the similarity of the female genitalia to those of *Holoarctia*. The scobinate juxta occurs only in *Holoarctia*, *Rhyparia*, and *Rhyparioides* of the taxa examined here, and also in *Hyperborea* (Ferguson 1985). This character appears to be a synapomorphy for the Arctiina *s.s.* The characters purportedly linking *Sonorarctia* to the PO group occur also in the Arctiini, although usually reduced or vestigial, such as the transtilla and flange of the vinculum; some Arctiini also lack the narrow apex of the uncus, e.g. *Parasemia*. Based on the available evidence, *Sonorarctia* is best placed in the Arctiina near *Apantesis*.

Virbia

The genus *Virbia*, including those species formerly placed in *Holomelina* (Zaspel and Weller 2006), possesses a number of unique synapomorphies (Forbes 1960, Ferguson 1985, Zaspel and Weller 2006), making their phylogenetic placement within the Arctiina *s.l.* uncertain. This led Forbes (1960) and Ferguson (1985) to recognize the genus as a distinct group within the Arctiina. Dubatolov (2003) placed *Virbia* with the Micrarctiina, although expressing uncertainty about this arrangement. Larval and non-genitalic characters placed *Virbia* nearest *Platyprepia* among the seven Arctiina genera examined by Jacobson and Weller (2002), which would suggest a close relationship to the Arctiina *s.s.* (as defined here). *Virbia* shares no apparent morphological characters with the Arctiina examined here, and grouped with the outgroup taxa *Cisseps*, *Cycnia* and *Gnophaela* in the morphology parsimony analysis (clade G, Fig. 4-4). Fourteen apomorphies were common to clade G, none unique to the clade (Table 4-2). Five of 14 apomorphies were common to both clade G (outgroup) and F (ingroup) (6: 1, 27: 0, 33: 0, 68: 2, 77: 0), and character 20 (absence of the hindwing M2 vein) was unique to *Virbia*. Six of the 14 clade G apomorphies were therefore ambiguous with respect to placement of Virbia in the ingroup versus outgroup. The remaining eight apomorphies all exhibited low consistency indices, although the presence of a swollen uncus base (45:1) occurred in *Virbia* and also *Cisseps* and *Cycnia* (CI = 0.50).

The single representative of *Virbia* included here did not group with the Arctiina *s.l.* in either the morphology or combined data sets (Figs. 4-4, 4-6), although placement in the Arctiina was not ruled out based on the *cox1* sequence data (Fig. 4-5). *Virbia* and *Pyrrharctia* (here placed in the Spilosomina) are the only arctiines known to produce female sex pheromones with methyl-branched hydrocarbons (Millar 2000). If *Virbia* truly belongs in the Arctiina *s.s.*, it would be the only member of this group with an extensive South American distribution. The taxonomic position of *Virbia* within the Arctiina *s.l.* remains uncertain, and additional taxon sampling and/or molecular data will be needed to shed light on this interesting situation, particularly in light of the scaphium/uncus interpretation discussed above.

CONCLUSIONS

The subtribe Arctiina has been variously treated as monophyletic, paraphyletic or consisting of more than one subtribe. The results presented here support the interpretation that the Spilosomina be treated as a subtribe separate from the Arctiina, united by two unique synapomorphies. This result provides a starting point for a more in-depth phylogeny of this group, consisting of about 70 genera globally. The monophyly of the remaining genera, Arctiina in the strict sense, was supported by five non-unique synapomorphies, and the phylogeny of the group therefore remains tentative and should be examined further. Although the placement of *Virbia* was problematic, it is best retained in the Arctiina until more characters and/or taxa can be examined. As defined here, the Arctiina includes 34 genera globally, with a Holarctic distribution (although *Notarctia* ranges south to Colombia, the only Arctiina genus ranging to the Neotropics; Ferguson 1985). The monophyly of the groups within the Arctiina *s.l.* proposed by Ferguson (1985) were not supported, with the exception of the *Arctia-Hyphoraia* group.

Summary of taxonomic implications

A) The genus *Grammia* Rambur as previously defined is not monophyletic, and *Grammia obliterata* (Stretch) is transferred to *Holarctia* M.E. Smith.

B) *Palearctia* Ferguson is synonymized under *Holarctia* M.E. Smith.

C) The *Phragmatobia-Ocnogyna* and *Spilosoma* groups of Ferguson (1985) are not reciprocally monophyletic, but together form a monophyletic group. As such, the genera of these groups, together with the *Spilarctia*-group genera of Kôda (1987), should be recognized as the Spilosomina.

D) The taxonomic groups thought to include *Grammia*, namely the *Neoarctia-Grammia* group of Ferguson (1985) and the Micrarctiina of Dubatolov (1996), were not supported as being monophyletic, and the remaining non-spilosomine Arctiina *s.l.* should therefore be retained in the Arctiina *sensu stricto*, including *Virbia*.

E) The genus *Kodiosoma* previously placed in the Arctiina is more closely related to *Cycnia* and *Euchaetes*, and is therefore transferred to the Phaegopterina.

List of North American genera previously placed in Arctiina (Franclemont 1983, Ferguson and Opler 2006). Taxon sequence follows that of Ferguson & Opler (2006).

ARCTIINA

VIRBIA Walker, 1854
HOLOARCTIA Ferguson, 1984
NEOARCTIA Neumögen and Dyar, 1893
HYPERBOREA Grum-Grshimailo, 1900
GRAMMIA Rambur, 1866
PALEARCTIA Ferguson, 1984
NOTARCTIA M. E. Smith, 1938
APANTESIS Walker, 1855
SONORARCTIA Ferguson, 1985
PARASEMIA Hübner 1816 [1820]
ACERBIA Sotavalta, 1963
PARARCTIA Sotavalta, 1965
PLATARCTIA Packard, 1864
PLATYPREPIA Dyar, 1897
ARCTIA Schrank, 1802

SPILOSOMINA[3]

PHRAGMATOBIA Stephens, 1828
LEPTARCTIA Stretch, 1874
PYRRHARCTIA Packard, 1864
SEIRARCTIA Packard, 1864
ESTIGMENE Hübner, 1816 [1820]
HYPHANTRIA Harris, 1841
SPILOSOMA Curtis, 1825
EUERYTHRA Harvey, 1876
ALEXICLES Grote, 1883
HYPERCOMPE Hübner, 1808
ARACHNIS Geyer, 1837

PHAEGOPTERINA

KODIOSOMA Stretch, 1874, **new subtribal placement**

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[3] all Spilosomina represent new subtribal placements

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Table 4-1. Collecting data, dissection numbers, voucher deposition and GenBank accession numbers of sampled taxa.

		Morphology					mtDNA					
Arctiina group*	Species	Dissection #	Locality †	Date	Collector	Voucher	Sample ID	GenBank accession number **	Locality	Date	Collector	Voucher §
Arctia-Hyphoraia Grp.	*Parasemia plantaginis* (L.)	BCS-3334	CAN: AB: Bilby	02-Jul-24	Bryant, O.	UASM	CGWC3843		CAN: BC: Hanceville	11-Jul-01	Guppy, C.S.	BIO
Arctia-Hyphoraia Grp.	*Arctia caja* (L.)	BCS-3353	CAN: AB: Cooking L., Franck farm	02-Aug-97	Lawrie, D.	UASM	BCSC61	EU119583	CAN: AB: Ministik Lake	09-Jul-99	Schmidt, B.C.	BCSC
Arctia-Hyphoraia Grp.	*Platarctia parthenos* (Harris)	BCS-3356	CAN: AB: Cooking L., Franck farm	11-Jun-98	Schmidt, B.C.	BCSC	BCSC396	EU119597	CAN: AB: Peace River, 8km NW	16-Jun-04	Hood, B.	BCSC
Arctia-Hyphoraia Grp.	*Platyprepia virginalis* (Bdvl.)	BCS-3352	CAN: BC: Crawford Bay	25-Jun-94	Schmidt, B.C.	BCSC	BCSC401	EU119598	CAN: BC: Riondel	-	Schmidt, B.C.	BCSC
Arctia-Hyphoraia Grp.	*Pararctia yarrowii* (Stretch)	BCS-3355	CAN: AB Wilcox Pass	21-Jul-71	Pike, E.M.	UASM	BCSC68	EU119595	CAN: AB: Mt. Tripoli, Cardinal Divide	18-Jul-99	Schmidt, B.C.	BCSC
Holomelina Grp.	*Virbia ferruginosa* (Wk.)	BCS-3319	CAN: AB: Edmonton	01-Jul-16	Bowman, K.	UASM	BCSC51	EU119591	CAN: AB: Lac La Biche, 20km N	05-Jul-97	Schmidt, B.C.	BCSC
Neoarctia-Grammia Grp.	*Holarctia obliterata* (Stretch)	BCS-3360	CAN: AB: Kootenay Plains ER, Whirlpool Pt.	26-Jul-06	Schmidt, B.C.; Dombroskie, J.	UASM	BCSC315	EU119467	CAN: AB: Dunvegan	14-Aug-03	Schmidt, B.C.	BCSC
Neoarctia-Grammia Grp.	*Grammia (Mimarctia) arge* (Drury)	BCS-3362	CAN: ON: Carp Ridge	02-Aug-03	Troubridge, J.T.	BCSC	BCSC239	EU119425	CAN: ON: Carp Ridge	18-Aug-03	Troubridge, J.	BCSC
Neoarctia-Grammia Grp.	*Grammia (Grammia) virgo* (L.)	BCS-3172	CAN: NS: Kentville	29-Jul-89	—	BCSC	BCSC354	EU119510	USA: TN: Cades Cove loop	25-Jul-00	Goldstein, P.	BCSC
Neoarctia-Grammia Grp.	*Chelis maculosa* (Gerning)	BCS-3335	ESP: Teruel, Fuente del Tajo	28-Jun-03	Rietz, H.	CNC	-	-	-	-	-	-
Neoarctia-Grammia Grp.	*Notarctia proxima* (G.-M.)	BCS-3354	USA: CA: San Luis Obispo Co., Montana de Oro St. Pk.	24-Apr-96	Landry, B. & J. Powell	CNC	BCSC272	EU119594	CR: Heredias: 11km SE La Virgen 450m	22-Feb-03	Heddle, M.; Powell, J.	BCSC
Neoarctia-Grammia Grp.	*Apantesis nais* (Drury)	BCS-3359	USA: NE: Omaha	—	Marshall, F.H.	UASM	CNCNoc_10148	EU119581	CAN: ON: Carp Ridge	16-Jun-04	Troubridge, J.	CNC

Table 4-1 (cont'd). Collecting data, dissection numbers, voucher deposition and GenBank accession numbers of sampled taxa.

		Morphology					mtDNA						
Arctiina group*	**Species**	**Dissection ‡**	**Locality †**	**Date**	**Collector**	**Voucher**	**Sample ID**	**GenBank #**	**Locality**	**Date**	**Collector**	**Voucher §**
Neoarctia-Grammia Grp.	*Holoarctia sordida* (McD.)	BCS-3361	CAN: AB: Kananasksis, Mt. Galatea	17-Aug-91	Lawrie, D.	UASM	BCSC399	EU119590	CAN: AB: Mt. Tripoli, Cardinal Divide	-	Schmidt, B.C.	BCSC
Neoarctia-Grammia Grp.	*Neoarctia beanii* (Neum.)	BCS-3323	CAN: AB: Nordegg	17-Jul-17	Bowman, K.	UASM	BCSC400	EU119593	CAN: AB: Hailstone Butte	12-Aug-04	Schmidt, B.C.	BCSC
Phragmatobia-Ocnogyna Grp.	*Phragmatobia assimilans* Wlk.	BCS-3363	CAN: AB: Rocky Mtn House, 30km N	07-Jun-97	Schmidt, B.C.; Lawrie, D.	BCSC	UASM24734	EU119596	CAN: AB: Redwater Natural Area	04-May-01	Schmidt, B.C.	UASM
Phragmatobia-Ocnogyna Grp.	*Ocnogyna loewii* (Zeller)	BCS-3321	RUS: Turkmenia, Kopetdag, Fiajuza	17-Oct-88	Zintshenko, V.	CNC	-	-	-	-	-	-
Phragmatobia-Ocnogyna Grp.	*Leptarctia californiae* (Wlk.)	BCS-3329	—	—	—	UASM	-	-	-	-	-	-
Spilosoma Grp.	*Rhyparia purpurata* (L.)	BCS-3324	DEU: —	—	Martin, C.	CNC	-	-	-	-	-	-
Spilosoma Grp.	*Rhyparioides amurensis* (Bremer)	BCS-3325	RUS: Primorye territory, Tigrovoi	11-Jul-76	Tshistjakov.	CNC	-	-	-	-	-	-
Spilosoma Grp.	*Diacrisia sannio* (L.)	BCS-3322	AUT: Tirol, Obergurgl	17-Jul-53	Vockeroth, J.R.	CNC	BCSC414	EU119584	RUS: Penza: Pobeda village	06-Jun-04	-	BCSC
Spilosoma Grp.	*Spilosoma virginica* (F.)	BCS-3326	CAN: BC: Riondel	09-May-94	Schmidt, B.C.	BCSC	HLC20545		CAN: BC: Glacier Nat. Pk., Rogers Pass Centre	04-Jul-05	Pickthorn, K.	BIO
Spilosoma Grp.	*Pyrrharctia isabella* (J.E. Smith)	BCS-3320	CAN: AB: Cooking L., Franck farm	19-Jun-98	Lawrie, D.	UASM	BCSC409	EU119599	USA: KY: Barren Co., Beaver Tr. Park	19-Jul-02	Cook, C.	BCSC
Spilosoma Grp.	*Estigmene acrea* (Drury)	BCS-3332	CAN: AB: Buffalo	16-Jun-05	Anweiler, G.	UASM	UASM57426	EU119586	CAN: AB: Oldman R. S of Vauxhall	18-May-05	Anweiler, G.	UASM
Spilosoma Grp.	*Arachnis picta* Packard	BCS-3364	MEX	—	—	BCSC	BCSC402	EU119582	USA: AZ: Tucson	01-Oct-05	Nagle, R.	BCSC

Table 4-1 (cont'd). Collecting data, dissection numbers, voucher deposition and GenBank accession numbers of sampled taxa.

		Morphology					mtDNA					
Arctiina group*	Species	Disection #	Locality †	Date	Collector	Voucher	Sample ID	GenBank #	Locality	Date	Collector	Voucher §
Outgroups												
Callimorphini	*Haploa lecontei* (G.-M.)	BCS-3333	CAN: AB: Cooking L., Franck farm	27-Jul-97	Lawrie, D.	UASM	UASM7031	EU119589	CAN: AB: Ministik Hills, 15km W Tofield	11-Jul-00	Schmidt, B.C.	UASM
Pericopini	*Gnophaela vermiculata* (Grote)	BCS-3365	CAN: AB: Didsbury	15-Jun-89	Schmidt, B.C.	BCSC	UASM43016	EU119587	CAN: AB: Edmonton, U of Alberta campus	10-Jul-98	Lawrie, D.	UASM
Phaegopterini	*Halysidota tessellaris* (J.E. Smith)	BCS-3350	USA: NY: New Windsor	17-Jul-93	Martin, E.L.	UASM	BCSC408	EU119588	USA: KY: Barren Co., Beaver Tr. Park	19-Jul-02	Cook, C.	BCSC
Phaegopterini	*Cycnia tenera* Hbn.	BCS-3351	CAN: AB: Oldman R., S of Vauxhall	18-May-06	Anweiler, G.	UASM	HLC20088		CAN: BC: Mt. Revelstoke Nat. Pk., Mt. Revelstoke base	18-Jun-05	Pickthorn, K.	BIO
Ctenuchini	*Cisseps fulvicollis* (Hbn.)	BCS-3358	CAN: AB: Tilley	01-Jul-41	Carr, J.L.	UASM	CGWC3837		CAN: BC: Quesnel	25-Jul-01	Guppy, C.S.	BIO
Lithosiinae	*Eilema bicolor* (Grt.)	BCS-3326	CAN: BC: Riondel	10-Aug-93	Schmidt, B.C.	BCSC	BCSC53	EU119585	CAN: BC: Riondel, 2km S	29-Jul-91	Schmidt, B.C.	BCSC
Lithosiinae	*Hypoprepia miniata* (Kirby)	BCS-3327	CAN: BC: Riondel	10-Aug-93	Schmidt, B.C.	BCSC	BCSC74	EU119592	CAN: AB: Redwater Nat. Area	20-Jul-99	Schmidt, B.C.	BCSC

* Arctiina group membership follows that of Ferguson (1985).

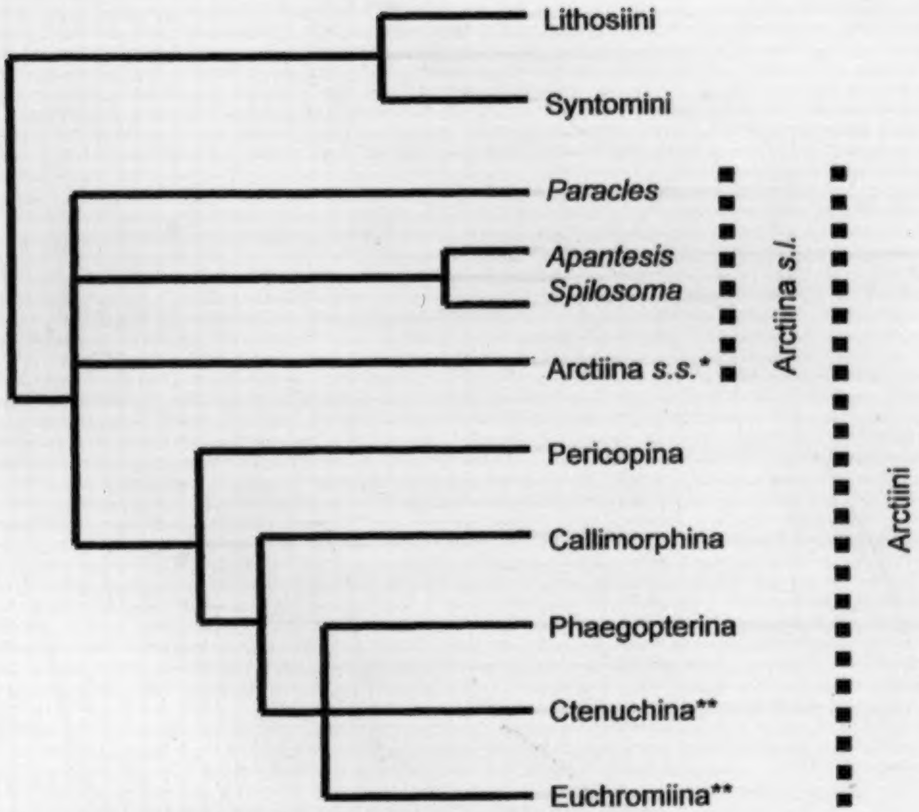
† Country abbreviations are as follows: AUT – Austria; CAN – Canada; DEU – Germany; MEX – Mexico; RUS – Russian Federation; USA – United States of America.

** Some accession numbers not available at time of writing.

§ Abbreviations for collections: BCSC - B. Christian Schmidt Personal Collection, Ottawa, Ontario; BIO: Biodiversity Institute of Ontario, University of Guelph, Ontario; CNC - Canadian National Collection of Insects, Ottawa, Ontario; UASM - University of Alberta Strickland Entomological Museum, Edmonton, Alberta.

Table 4-2. Morphology apomorphies for major clades, optimized on morphology tree topology (Fig. 4-4). Chararcters in bold indicate unique synapomorphies.

Clade	Character	State Change	CI
A	49	2 to 1	0.30
Arctia grp.**50**		0 to 2	1.00
	60	1 to 2	0.38
B	18	1 to 0	0.17
Grammia grp.	26	1 to 0	0.20
	68	1 to 0	0.33
	71	1 to 0	0.33
	76	0 to 1	0.20
C	7	1 to 2	0.29
Neoarctia grp.	8	1 to 0	0.20
	42	0 to 1	1.00
	55	1 to 0	0.25
	58	1 to 0	0.33
	63	1 to 0	0.33
	67	2 to 1	0.22
D	7	0 to 1	0.29
Arctiina *s.s.*	9	1 to 0	0.20
	22	1 to 0	0.25
	67	1 to 2	0.22
	68	2 to 1	0.33
E	7	0 to 1	0.29
Spilosomina	8	1 to 0	0.20
	9	1 to 0	0.20
	14	0 to 1	0.50
	22	1 to 0	0.25
	29	0 to 1	1.00
	31	0 to 1	1.00
	39	0 to 1	0.25
	43	0 to 1	0.33
	52	0 to 1	0.33
	60	1 to 2	0.38
	68	2 to 1	0.33
F	18	0 to 1	0.17
Arctiina +	26	0 to 1	0.20
Spilosomina	32	1 to 0	0.50
(Arctiina *s.l.*)	53	0 to 1	0.25
	55	0 to 1	0.25
	73	1 to 0	0.33
	76	1 to 0	0.20
G	**6**	0 to 1	1.00
Virbia +	18	0 to 1	0.17
outgroups	**20**	1 to 0	1.00
	26	0 to 1	0.20
	27	1 to 0	0.50
	33	1 to 0	0.50
	45	0 to 1	0.50
	57	0 to 2	0.40
	62	0 to 1	0.33
	67	1 to 2	0.22
	68	1 to 2	0.33
	73	1 to 0	0.33
	76	1 to 0	0.20
	77	1 to 0	0.25


Lithosiini
Syntomini
Paracles
Apantesis
Spilosoma
Arctiina *s.s.**
Pericopina
Callimorphina
Phaegopterina
Ctenuchina**
Euchromiina**
Arctiina *s.l.*
Arctiini

* sampled taxa consisted of *Phragmatobia, Pyrrharctia, Virbia,Platyprepia*

** not reciprocally monophyletic (Simmons & Weller 2001)

Figure 4-1. Composite phylogeny of the Arctiini, based Jacobson & Weller (2002) and DaCosta & Weller (2005), with nomenclature adjusted to reflect Lafontaine & Fibiger (2006).

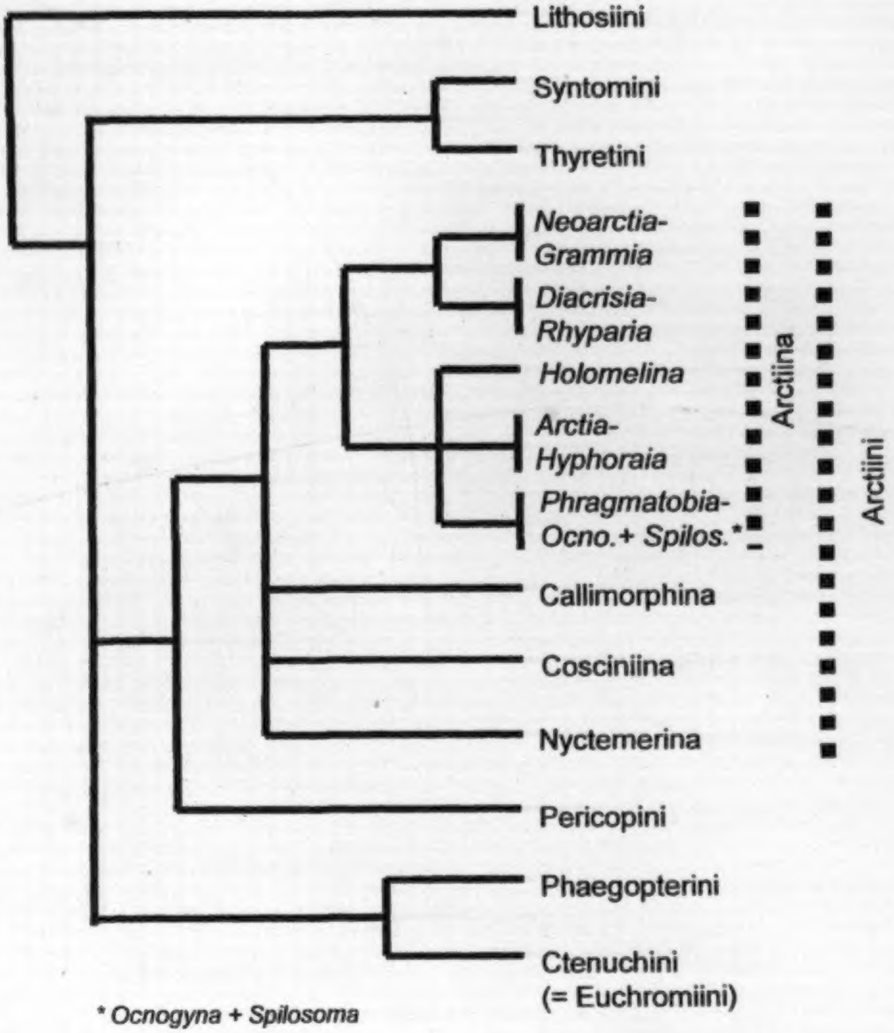

Lithosiini
Syntomini
Thyretini
Neoarctia-Grammia
Diacrisia-Rhyparia
Holomelina
Arctia-Hyphoraia
Phragmatobia-Ocno.+ Spilos.*
Callimorphina
Cosciniina
Nyctemerina
Pericopini
Phaegopterini
Ctenuchini (= Euchromiini)
Arctiina
Arctiini
* Ocnogyna + Spilosoma

Figure 4-2. Phylogeny of the Arctiini inferred from Bendib & Minet (1998), based largely on female genitalic and pheromone gland structure.

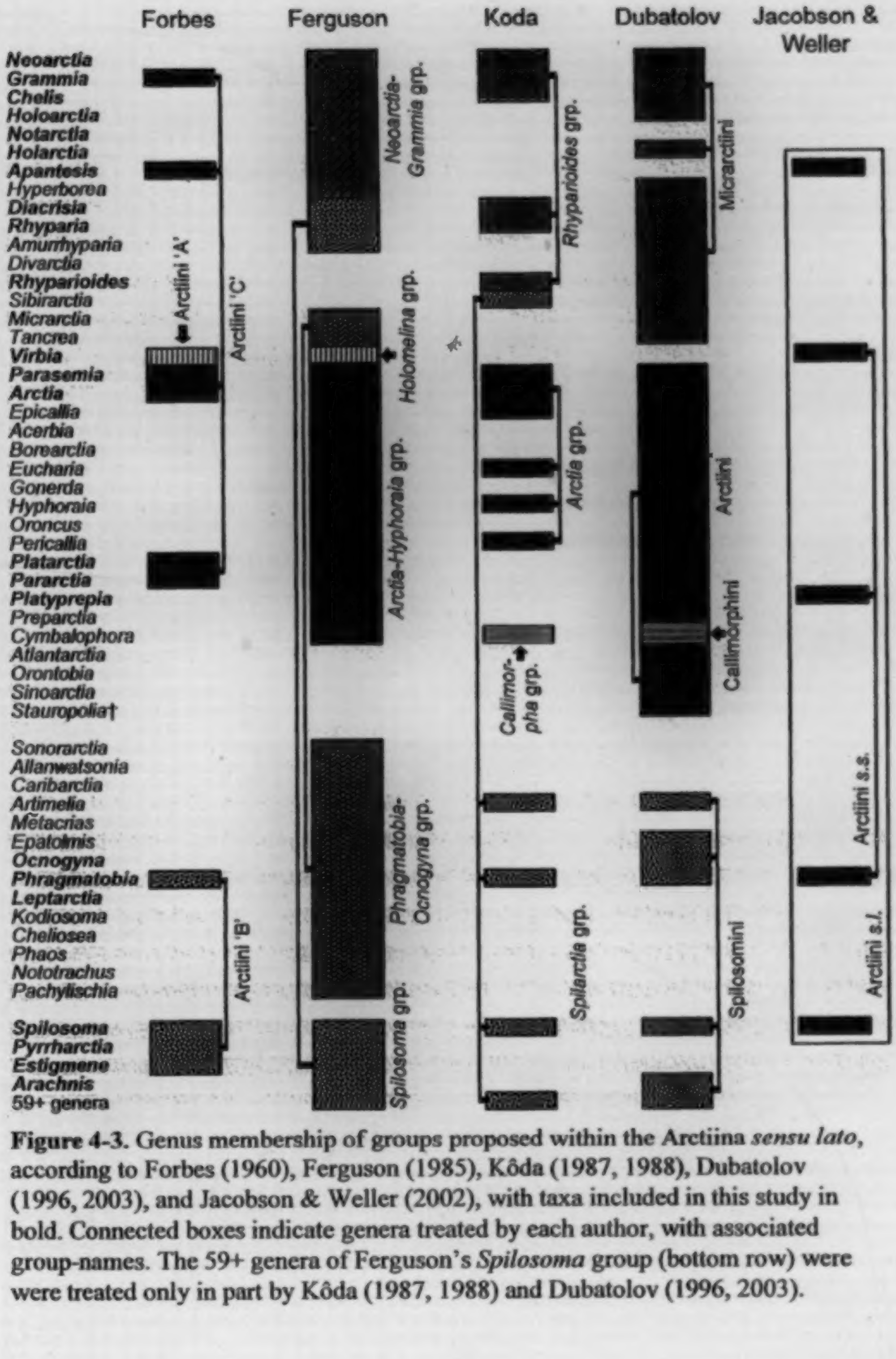

Forbes
Ferguson
Koda
Dubatolov
Jacobson & Weller
Neoarctia
Grammia
Chelis
Holoarctia
Notarctia
Holarctia
Apantesis
Hyperborea
Diacrisia
Rhyparia
Amurrhyparia
Divarctia
Rhyparioides
Sibirarctia
Micrarctia
Tancrea
Virbia
Parasemia
Arctia
Epicallia
Acerbia
Borearctia
Eucharia
Gonerda
Hyphoraia
Oroncus
Pericallia
Platarctia
Pararctia
Platyprepia
Preparctia
Cymbalophora
Atlantarctia
Orontobia
Sinoarctia
Stauropolia†
Sonorarctia
Allanwatsonia
Caribarctia
Artimelia
Metacrias
Epatolmis
Ocnogyna
Phragmatobia
Leptarctia
Kodiosoma
Cheliosea
Phaos
Nototrachus
Pachylischia
Spilosoma
Pyrrharctia
Estigmene
Arachnis
59+ genera
Arctiini 'A'
Arctiini 'C'
Arctiini 'B'
Neoarctia-Grammia grp.
Holomelina grp.
Arctia-Hyphoraia grp.
Phragmatobia-Ocnogyna grp.
Spilosoma grp.
Rhyparioides grp.
Arctia grp.
Callimorpha grp.
Spilarctia grp.
Micrarctiini
Arctiini
Callimorphini
Spilosomini
Arctiini s.s.
Arctiini s.l.

Figure 4-3. Genus membership of groups proposed within the Arctiina *sensu lato*, according to Forbes (1960), Ferguson (1985), Kôda (1987, 1988), Dubatolov (1996, 2003), and Jacobson & Weller (2002), with taxa included in this study in bold. Connected boxes indicate genera treated by each author, with associated group-names. The 59+ genera of Ferguson's *Spilosoma* group (bottom row) were were treated only in part by Kôda (1987, 1988) and Dubatolov (1996, 2003).

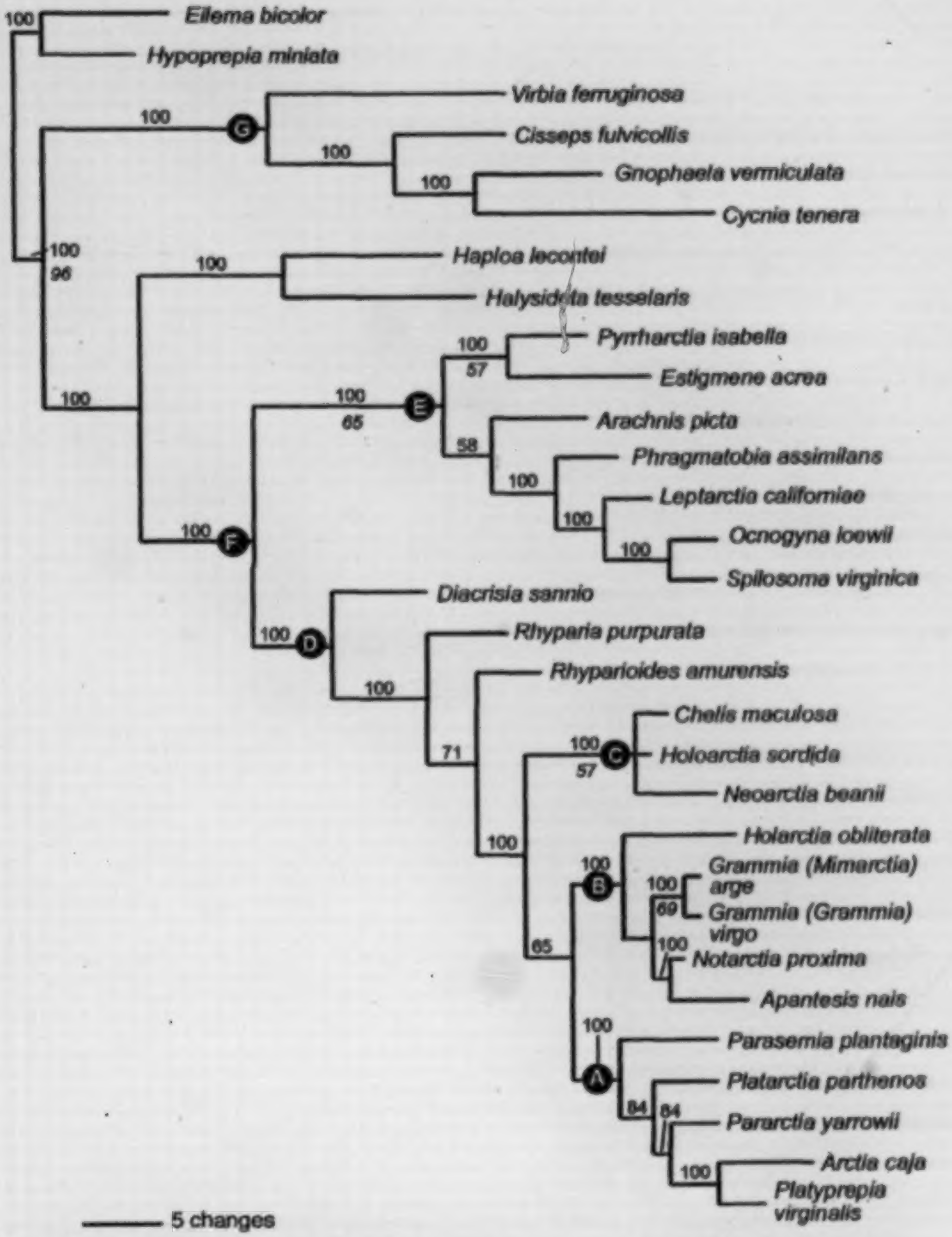

100
Eilema bicolor
Hypoprepia miniata
100
G
Virbia ferruginosa
100
Cisseps fulvicollis
100
Gnophaela vermiculata
Cycnia tenera
100
96
100
Haploa lecontei
Halysidota tesselaris
100
57
Pyrrharctia isabella
Estigmene acrea
100
100
65
E
Arachnis picta
58
Phragmatobia assimilans
100
Leptarctia californiae
100
Ocnogyna loewii
100
Spilosoma virginica
100
F
Diacrisia sannio
100
D
Rhyparia purpurata
100
Rhyparioides amurensis
71
Chelis maculosa
100
57
C
Holoarctia sordida
Neoarctia beanii
100
Holarctia obliterata
100
B
Grammia (Mimarctia) arge
100
69
Grammia (Grammia) virgo
100
Notarctia proxima
Apantesis nais
65
100
Parasemia plantaginis
A
Platarctia parthenos
84
84
Pararctia yarrowii
100
Arctia caja
Platyprepia virginalis
5 changes

Figure 4-4. Maximum parsimony phylogram based on 81 morphological characters, shown as the majority-rule consensus of 21 most parsimonious trees (Tree length 262, Consistency Index 0.37, Retention Index 0.66). Values above branches indicate majority-rule consensus frequencies above 50%, bootstrap support values are given below branches. Letters indicate major clades referred to in Table 4-2 and in text.

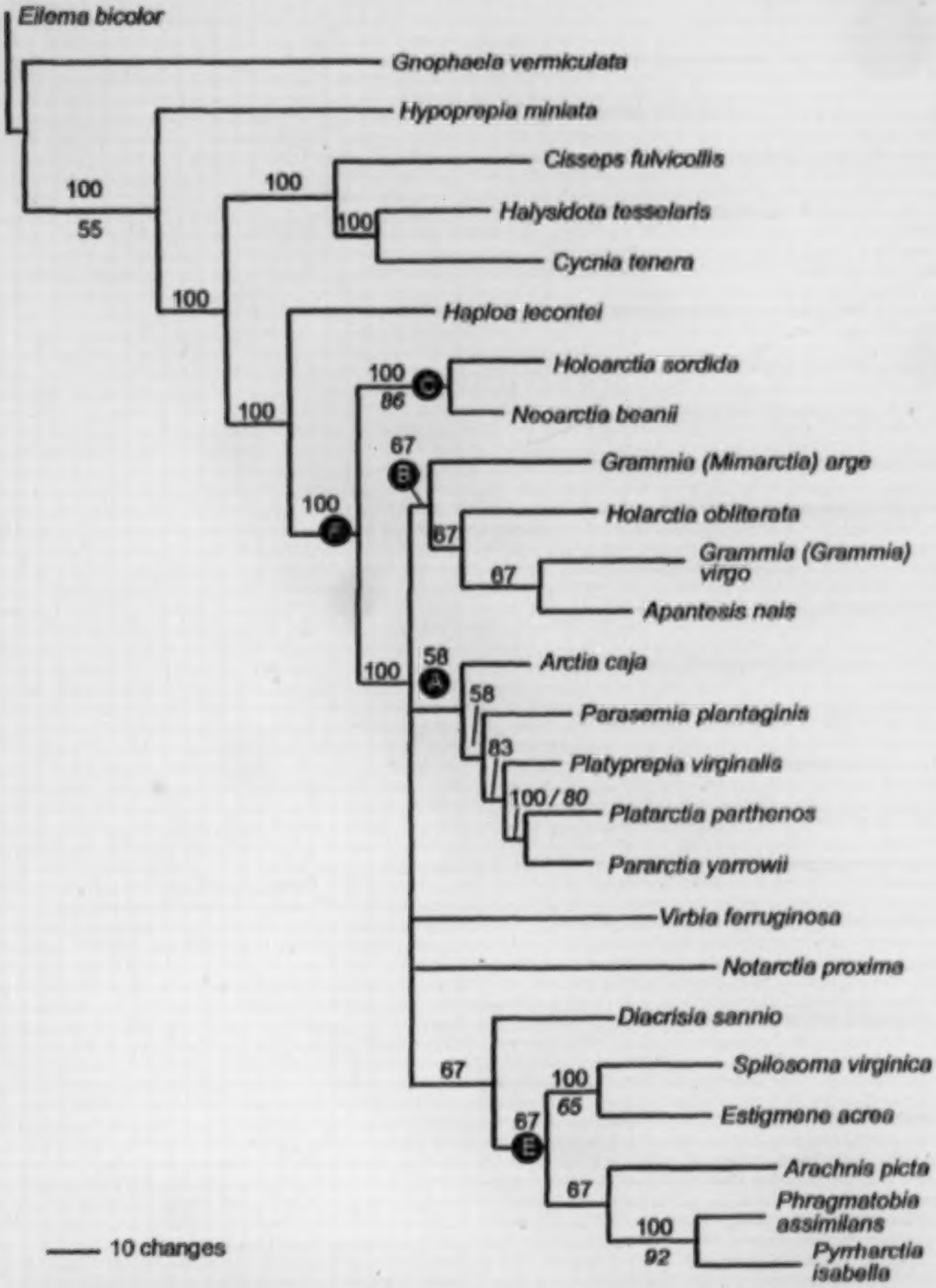

Eilema bicolor
Gnophaela vermiculata
Hypoprepia miniata
Cisseps fulvicollis
100
100
55
100
Halysidota tesselaris
Cycnia tenera
100
Haploa lecontei
100
C
86
Holoarctia sordida
100
Neoarctia beanii
67
B
Grammia (Mimarctia) arge
100
F
Holarctia obliterata
67
Grammia (Grammia) virgo
67
Apantesis nais
58
A
Arctia caja
100
58
Parasemia plantaginis
83
Platyprepia virginalis
100 / 80
Platarctia parthenos
Pararctia yarrowii
Virbia ferruginosa
Notarctia proxima
Diacrisia sannio
67
100
Spilosoma virginica
65
67
E
Estigmene acrea
Arachnia picta
67
Phragmatobia assimilans
100
92
Pyrrharctia isabella
10 changes

Figure 4-5. Maximum parsimony phylogram based on 658 bp 'barcode' fragment of *cox1*, shown as the majority-rule consensus of 12 most parsimonious trees (Tree length 769, Consistency Index 0.41, Retention Index 0.33). Values above branches indicate majority-rule consensus frequencies above 50%, bootstrap support values are given below branches. Letters indicate major clades referred to in Table 4-2 and in text.

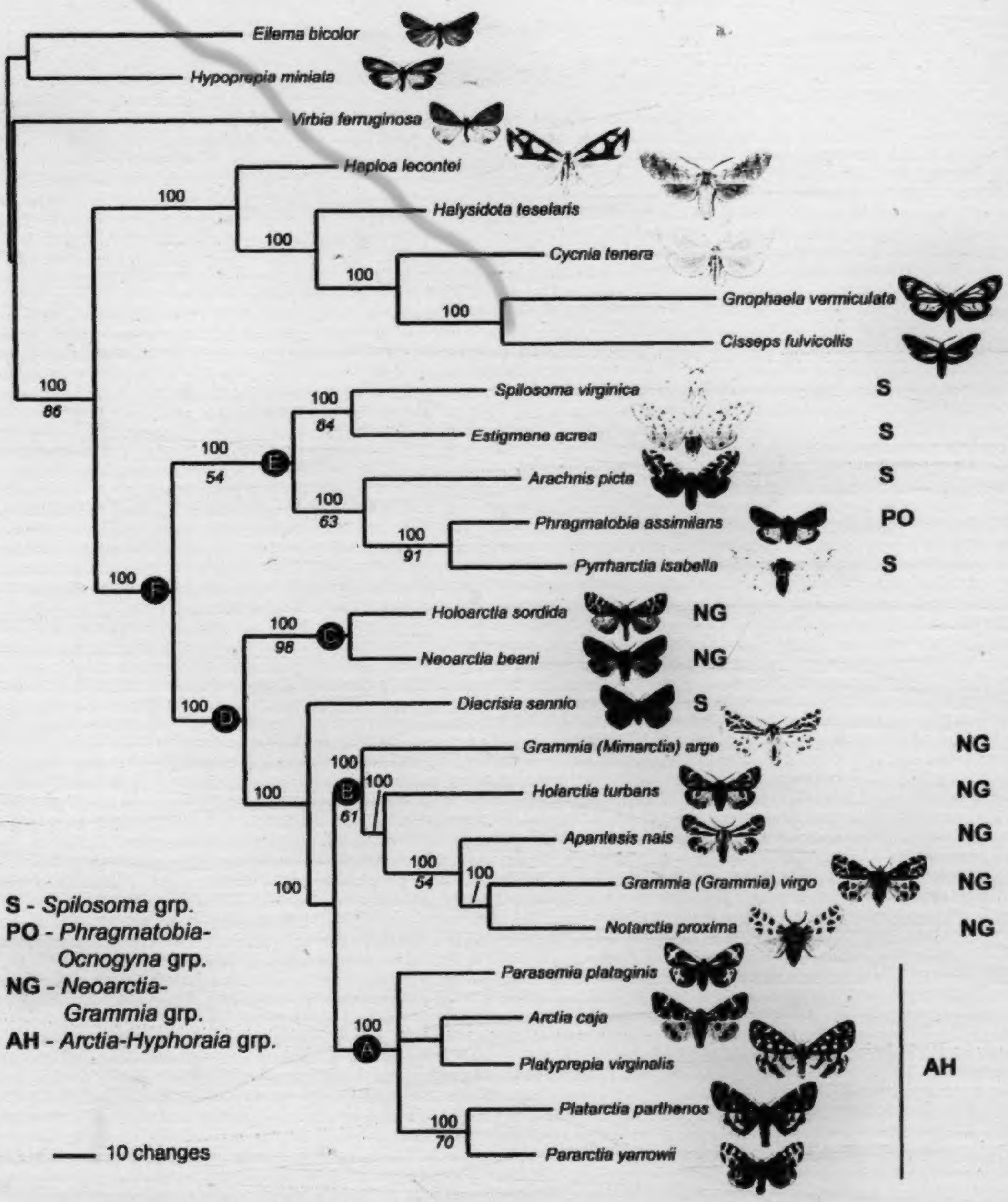

Eilema bicolor
Hypoprepia miniata
Virbia ferruginosa
Haploa lecontei
Halysidota teselaris
Cycnia tenera
Gnophaela vermiculata
Cisseps fulvicollis
Spilosoma virginica
Estigmene acrea
Arachnis picta
Phragmatobia assimilans
Pyrrharctia isabella
Holoarctia sordida
Neoarctia beani
Diacrisia sannio
Grammia (Mimarctia) arge
Holarctia turbans
Apantesis nais
Grammia (Grammia) virgo
Notarctia proxima
Parasemia plataginis
Arctia caja
Platyprepia virginalis
Platarctia parthenos
Pararctia yarrowii
S
S
S
PO
S
NG
NG
S
NG
NG
NG
NG
NG
AH
A
B
C
D
E
F
100
86
100
100
100
100
100
54
100
84
100
63
100
91
100
100
98
100
100
100
100
61
100
100
54
100
100
100
100
70
S - Spilosoma grp.
PO - Phragmatobia-Ocnogyna grp.
NG - Neoarctia-Grammia grp.
AH - Arctia-Hyphoraia grp.
10 changes

Figure 4-6. Maximum parsimony phylogram based on combined morphological and *cox1* 'barcode' data, shown as the majority-rule consensus of two most parsimonious trees (Tree length 1036, Consistency Index 0.40, Retention Index 0..37). Values above branches indicate majority-rule consensus frequencies above 50%, bootstrap support values are given below branches. Letters on internal branches indicate major clades referred to in Table 4-2 and text. Genus-group names refer to those of Ferguson (1985).

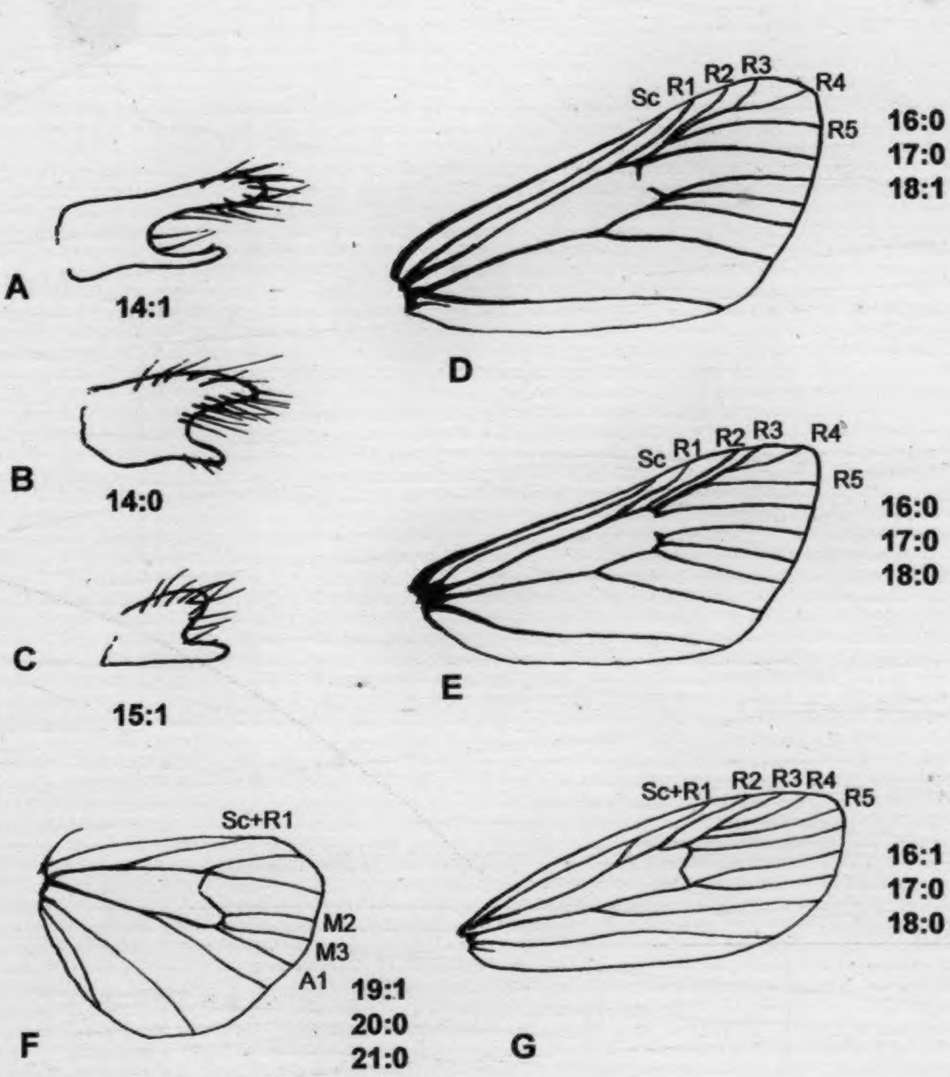

A
14:1
B
14:0
C
15:1
Sc
R1
R2
R3
R4
R5
16:0
17:0
18:1
D
Sc
R1
R2
R3
R4
R5
16:0
17:0
18:0
E
Sc+R1
M2
M3
A1
19:1
20:0
21:0
F
Sc+R1
R2
R3
R4
R5
16:1
17:0
18:0
G

Figure 4-7. Characters and states of foretarsal flaps (A-C) and wing venation (D-G) of Arctiinae. **A.** *Pyrrharctia isabella*; **B.** *Arctia caja*; **C.** *Gnophaela vermiculata*; **D.** forewing venation of *Neoarctia sordida*; **E.** forewing venation of *Grammia virgo*; **F.** forewing venation of *Eilema bicolor*; **G.** hindwing venation of *Phragmatobia assimilans*.

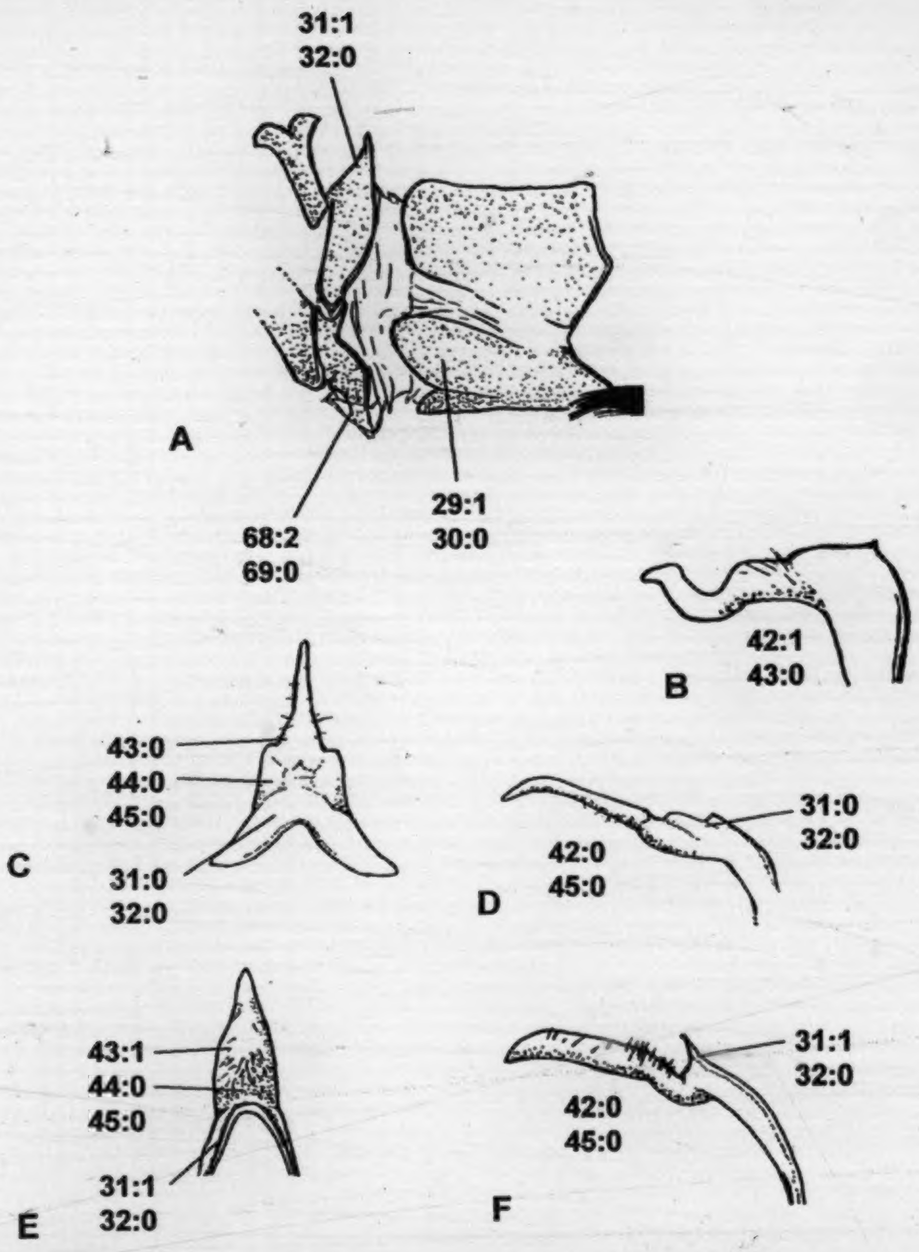

31:1
32:0
A
68:2
69:0
29:1
30:0
42:1
43:0
B
43:0
44:0
45:0
C
31:0
32:0
31:0
32:0
42:0
45:0
D
43:1
44:0
45:0
31:1
32:0
E
42:0
45:0
31:1
32:0
F

Figure 4-8. Characters and states of genitalic and abdominal structures of Arctiini. **A.** right lateral view of abdominal segment 8 and base of genitalic capsule of *Pyrrharctia isabella*; **B.** right lateral view of uncus and dorsal tegumen of *Chelis maculosa*; **C.** dorsal view of uncus and dorsal tegumen of *Grammia virgo;* **D.** same, right lateral view; **E.** dorsal view of uncus and dorsal tegumen of *Phragmatobia assimilans;* F. same, right lateral view.

Appendix 4-1. List of morphological and physiological characters. "JW" and "DW" indicate characters used in Jacobson & Weller (2002) and DaCosta & Weller (2006) respectively; an asterisk indicates characters used previously, but modified here. "UI" indicates parsimony uninformative characters.

1. Winter diapause: larval (0), pupal (1), does not apply or unkown (?).

2. (DW2*) Male antennae: bipectinate (0), filiform (1).

3. Male antennal segments longer than wide: absent (0), present (0).

4. (UI) Number of antennal segments: less than 50 (0), greater than 50 (1).

5. Width of antennal pedicel: less than 1.5 times width of 1st antennal segment (0), more than 1.5 times width of 1st antennal segment (1).

6. (DW3, JW38) Ocellus: absent (0), present (1).

7. (DW5, JW41). Proboscis length: longer than length of thorax (0), shorter than thorax but longer than height of head (1), shorter than height of head (2).

8. Second segment of labial palp length: shorter than 1st (0), greater than or equal to 1st (1).

9. Third segment of labial palp length: greater than or equal to half length of 2nd (0), less than half the length of 2nd.

10. (DW7*, JW40*) Tentorial crest: swollen (0), narrow (1).

11. (DW8*) Outer protibial claw: absent (0), present (1).

12. Inner protibial claw: absent (0), present (1).

13. (DW9, JW 45) Epiphysis length: greater than or equal to 2/3 length of foretibia (0), less than 2/3 length of tibia (1).

14. Shape of membranous flap adjacent to protarsal claw: stout (0), elongate (1).

15. (UI) Membranous flap adjacent to protarsal claw distinctly trilobed: absent (0), present (1).

16. (UI; DW13, JW32) Forewing veins Sc and R1: joining cell separately (0), anastamosing, forming areole (1).

17. (UI) Forewing veins R1 and R2: arising separately from discal cell (0), stalked (1).

18. Forewing veins R2 and R3: arising separately from discal cell (0), connate or stalked (1).

19. (DW18, JW34) Hindwing vein Sc+R1: absent (0), present (1), reduced (2).

20. (DW20, JW36) Hindwing vein M2 and M3: free of each other (0), stalked (1), M2 lost/fused (2).

21. (UI; DW21) Hindwing veins M3 and A1: separate (0), stalked (1).

22. (DW35*, JW48*) Tymbal microstriae: absent (0), present (1).

23. (DW36) Tympanal hood size: absent (0), average (1), large (2), reduced (3) (illustrated in DaCosta & Weller 2005).

24. (UI; DW37) Tympanal hood location: prespiracular (0), postspiracular (1), absent (2).

25. (DW46) Counter-tympanal hood: small (0), large (1) (illustrated in DaCosta & Weller 2005).

26. Male antecostal sclerite of abdominal sternite 8: absent (0), present (1).

27. Intersegmental membrane of abdominal sternites 8 and 9: shorter than sternite 7, greater than or equal to sternite 7 (1).

28. (DW 56) 8th tergite length: less than or equal to 7th tergite (0), greater than 7th tergite (1).

29. Lateral lobe of 8th sternite: absent (0), present (1).

30. (UI) Lateral lobe of 8th sternite unsclerotized (0) sclerotized (1).

31. Shape of dorsum of tegumen: flat/collar-like (0), produced dorsally or dorsocaudally (1).

32. Dorsum of tegumen expanded proximally into rounded areas: absent (0), present (1).

33. (DW60) Tegumen / Vinculum junction without distinct membranous break (0), with membranous break (1).

34. Lateral flange of vinculum: absent or vestigial (0), well-developed (1).

35. (UI) Tegumen with finger-like caudal projections: absent (0), present (1).

36. (DW61) Tegumen / uncus junction: membranous (0), fused (1).

37. (UI; DW62) Apex of uncus: simple (0), bifid (2).

38. Long setae (>0.3 mm) on uncus: absent / sparse (0), conspicuous (1).

39. Short setae (<0.3 mm) of uncus: absent / sparse (Fig. 4-8c,d) (0), conspicuous (Fig. 4-8e,f) (1).

40. Long (>0.3 mm) setae beyond basal half of uncus: absent (0), present (1).

41. (UI) Short setae (<0.3 mm) beyond basal half of uncus: absent (0), present (1).

42. Uncus flat or down-curving in lateral view (0), sinuate in lateral view (1).

43. Uncus with pronounced basal constriction (0), broad or slightly concave laterally (1).

44. (UI; DW64) Uncus with basal ornamentation: absent (0), present (1).

45. (DW66) Uncus base: unlobed (0), lobed or swollen (1).

46. Uncus dorsoventrally flattented or cylindrical, (0), laterally compressed and ridge-like (1).

47. (DW67) Scaphium: absent (0), present (1).

48. (UI) Subscaphium: absent (0), present (1).

49. (DW68) Transtilla: absent (0), well-developed (1), reduced (2).

50. Transtillar fingers: absent (0), present, not scobinate (1), present, scobinate (2).

51. (DW69) Annellus dorsum: membranous (0), sclerotized (1).

52. (DW70) Annellus ventrum: membranous (0), sclerotized (1).

53. (DW71) Manica: membranous (0), reinforced (1).

54. Juxta: at least as wide as high (0), narrower than height (1).

55. Juxta dorsal margin: emarginate (0), straight or slightly convex (1), sinuate (2).

56. Juxta ventral margin: rounded / entire (0), lobed or cleft (1).

57. Juxta lateral margin: parallel (0), constricted, tapering apically (1).

58. Juxta smooth (0), scobinate (1).

59. Juxta with convex longitudinal fold or ridge (somewhat roof-like): absent (0), present (1).

60. Valve beyond clasper: absent or highly reduced (0), lobate (1), cylindrical or quadrate elongate (2), bifurcate (3).

61. Valve inner surface smooth (0), with medial ridge or lobe (1).

62. Basal valve of inner surface: membranous (0), sclerotized (1).

63. Valve outer surface: evenly sclerotized (0), with membranous or poorly sclerotized break (1).

64. Valve outer surface without membranous lobe (0), with membranous lobe (1).

65. Valve costa: undifferentiated (0), with dorsal process (1).

66. Sacculus: unmodified (0), with lobe projecting medially (1).

67. (DW82) Saccus shape: conjunctiva (0), v-shaped (1), rounded (2).

68. Saccus length: greater than height of vinculum (0), ½ to equal vinculum height (1), less than ½ height of vinculum (2).

69. Ventral covering of saccus: membranous (0), reinforced or sclerotized (1).

70. (DW83) Aedeagus carina penis: absent (0), present (1).

71. Aedeagus apex: not scobinate (0), scobinate (1).

72. Aedeagus apex cornuti: absent (0), present (1).

73. Aedeagus opening with caudal component: absent (0), present (1).

74. Aedeagus opening with right lateral component: absent (0), present (1).

75. Aedeagus opening with left lateral component: absent (0), present (1).

76. Aedeagus length: long, greater than or equal to 5x width (0), short, less than 5x longer than wide (1).

77. Vesica with cornuti: absent (0), present (1).

78. Vesica length: less than or equal to ½ length of aedeagus (0), greater than ½ length of aedeagus but not exceeding aedeagus length (1), exceeding length of aedeagus (2).

79. Caecum penis: shorter than wide (0), longer than wide (1).

80. Caecum penis shape: rounded (0), conical (1).

81. (UI) Caecum penis without cleft proximal end (0), with cleft (1).

Appendix 4-2. Morphology character matrix.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Holarctia obliterata	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Grammia arge	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Grammia virgo	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Chelis	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	2	0
Notarctia proxima	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Apantesis nais	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Holoarctia sordida	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	2	0
Neoarctia beani	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Rhyparia purpurata	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Rhyparioides amurensis	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Diacrisia sannio	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parasemia plantaginis	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	2
Arctia caja	0	0	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Platarctia parthenos	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	2
Platyprepia virginalis	0	1	0	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Pararctia yarrowii	0	0	0	0	0	1	1	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Virbia ferruginosa	0	1	1	0	0	1	1	1	0	0	0	0	1	0	0	0	1	1	1	2	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	1	0	1	1	1	0	0	0
Phragmatobia assimilans	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	1	0	0	1	0	0	1	0	1	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0
Ocnogyna loewii	?	0	0	0	0	1	2	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0
Leptarctia californiae	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0	0	1	0	1	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0
Spilosoma virginica	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	1	1	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	2	0
Pyrrharctia isabella	0	1	0	0	0	1	1	0	0	1	1	1	1	1	0	0	0	1	1	0	0	1	1	0	0	1	1	0	1	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Estigmene acrea	1	0	0	0	0	1	1	0	0	1	1	1	1	1	0	0	0	1	1	0	0	0	1	0	0	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Arachnis picta	0	1	0	0	0	1	2	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	0	0	1	0	1	1	0	1	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0
Haploa lecontei	0	1	1	0	0	1	0	1	1	0	0	0	1	0	0	0	0	1	1	0	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	1	0
Gnophaela vermiculata	0	0	0	0	1	1	0	1	0	1	0	0	0	0	1	0	0	0	1	0	1	1	?	0	1	0	0	0	0	0	0	1	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Halysidota edwardsii	1	0	0	1	1	1	0	1	1	0	0	0	1	0	0	0	0	0	2	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	2	0	0	0	0	0	3	0
Cycnia tenera	1	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	1	1	1	0	0	1	0
Cisseps fulvicollis	0	0	0	0	1	1	0	1	1	1	0	0	1	0	0	0	0	1	0	0	0	1	2	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Ellema bicolor	0	1	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0	1	0	1	0	0	0	0	1	1	0	0	0
Hypoprepia miniata	0	1	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	1	1	0	1	0	2	1	0	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0

Appendix 4-2 (cont'd.). Morphology character matrix.

	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81
Holarctia obliterata	0	0	1	1	2	0	1	0	0	1	0	0	1	0	0	1	1	0	0	0	1	0	0	1	0	0	0	1	0	0	0
Grammia arge	0	0	1	1	0	1	0	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	0
Grammia virgo	0	0	1	0	0	1	0	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	0
Notarctia proxima	0	0	1	1	1	1	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	1	0	1	0	0	0
Apantesis nais	0	0	1	1	1	1	2	0	0	1	0	0	1	0	0	0	1	1	0	1	0	1	1	0	0	1	0	1	0	0	0
Holoarctia sordida	0	0	1	1	0	1	0	1	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	1	0	0	0
Neoarctia beani	0	0	1	1	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Rhyparia purpurata	0	0	0	1	1	1	0	1	0	1	2	0	1	0	0	0	2	1	0	0	1	0	0	1	0	0	0	1	0	0	0
Rhyparioides amurensis	0	0	1	1	1	1	0	1	0	1	0	0	1	0	0	0	2	1	0	0	1	0	0	1	0	1	0	1	0	0	0
Diacrisia sannio	0	0	1	0	1	1	0	0	0	1	2	0	1	0	0	0	2	1	0	0	0	0	0	1	0	0	0	1	0	0	0
Parasemia plantaginis	0	0	1	1	2	0	2	0	0	2	0	0	1	0	0	0	1	1	0	0	1	0	0	1	0	0	0	1	0	0	0
Arctia caja	0	0	1	1	1	1	0	0	1	2	0	0	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0
Platarctia parthenos	0	0	1	1	1	1	0	0	1	2	0	0	1	0	0	0	2	1	0	0	1	0	0	0	1	0	0	1	0	0	0
Platyprepia virginalis	0	0	1	1	1	1	0	0	1	2	0	0	1	0	0	1	1	1	0	0	1	0	0	1	0	0	0	1	0	0	0
Pararctia yarrowii	0	0	1	1	0	1	0	0	1	2	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	1	0	0	0
Virbia ferruginosa	0	0	0	1	0	0	2	0	0	2	0	1	0	0	0	0	2	2	0	0	0	1	0	0	0	0	0	1	1	0	1
Phragmatobia assimilans	0	1	0	0	1	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	1	0	0
Ocnogyna loewii	0	1	0	0	1	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Leptarctia californiae	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Spilosoma virginica	0	1	0	0	?	0	0	0	0	3	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	1	1	0	0
Pyrrharctia isabella	1	0	1	0	1	0	0	0	0	2	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	1	0
Estigmene acrea	0	1	1	0	?	0	0	0	0	2	0	0	0	0	0	1	2	1	0	0	0	0	0	0	0	0	1	1	1	0	0
Arachnis picta	0	1	1	0	?	0	0	0	0	2	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0
Haploa lecontei	1	0	1	1	1	0	0	0	0	3	0	1	0	1	0	0	2	2	0	0	0	0	1	0	0	1	0	1	1	1	0
Gnophaela vermiculata	1	1	1	0	?	2	2	0	0	1	0	1	0	0	0	0	1	2	1	0	0	0	0	1	0	0	0	0	0	0	0
Halysidota edwardsii	1	0	1	1	?	2	0	0	0	0	0	0	0	0	1	0	1	2	0	0	0	0	0	0	0	0	0	1	0	0	0
Cycnia tenera	1	1	1	0	?	2	2	0	0	0	0	1	0	1	0	0	2	2	1	1	0	0	0	0	0	0	0	0	1	1	0
Cisseps fulvicollis	0	1	0	0	?	0	2	0	0	?	0	0	0	0	?	?	2	2	1	0	0	0	0	1	0	1	0	2	0	0	0
Ellema bicolor	0	0	0	0	2	?	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	1	1	1	0	1	0
Hypoprepia miniata	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	1	1	1	0	0	0

Chapter 5.

General Conclusions.

Species of the genus *Grammia* Rambur (Lepidoptera: Noctuidae: Arctiinae) represent the most diverse species radiation of tiger moths in North America, yet their taxonomy remains poorly resolved, as a result of conserved morphology and considerable intraspecific variation in colour and pattern. Despite the broad habitat and geographic range at the generic level, most *Grammia* species are habitat-specific, and several taxa occur locally and/or in disjunct populations in western North America, and their taxonomic status is therefore particularly relevant from a conservation perspective. I explored a variety of character sets in an effort to identify taxonomically informative traits. Through a combination of morphological, ecological behavioural and molecular traits, I revised the species-level taxonomy of the genus in Chapter 2, and evaluated the phylogeny of *Grammia* and related genera. Six species, *Grammia margo* sp. nov., *G. yukona* sp. nov., *G. brillians* sp. nov., *G. fergusoni* sp. nov., *G. yavapai* sp. nov. and *G. ursina* sp. nov. are described, in addition to three new subspecies *G. virguncula celineata* ssp. nov., *G. virgo gigas* ssp. nov., and *G. nevadensis vivida* ssp. nov. *"Grammia" obliterata* (Stretch), previously treated as the monotypic subgenus *Holarctia*, is transferred to the genus previously recognized as *Palearctia* Ferguson, which is revised as a junior synonym of *Holarctia* M.E. Smith. *Grammia celia* (Saunders) is synonymized under *Grammia figurata* (Drury), and *Grammia franconia* (H. Edwards) is raised to species status. *Apantesis favorita* ab. *favoritella* Strand is revised to synonymy under *Grammia phyllira* (Drury). *Arctia speciosa* Möschler is revised to subspecies status under *Grammia virguncula* (Kirby).

Sequence analysis of the mitochondrial DNA cytochrome oxidase I gene proved to be of limited taxonomic value due to extensive gene tree non-monophyly. Species-level polyphyly of mtDNA phylogenies is not uncommon, and a number of causes can result in gene tree polyphyly (Funk and Omland 2003). In Chapter 3, I evaluate the possible causes of mtDNA polyphyly in *Grammia*, and propose that the most parsimonious explanation for this phenomenon is taxonomically and geographically widespread introgression of mtDNA resulting from hybridization events. This hypothesis could be tested in a number of ways, and *Grammia* would be a fascinating study system to further test the extent and importance of gene exchange in the face of species boundaries and reproductive barriers.

Extensive mtDNA polyphyly among a speciose, widespread group also highlights the inherent dangers of drawing phylogenetic, taxonomic, or biogeographic conclusions based solely on mtDNA (Hebert et al. 2003; Hebert et al. 2004; Hajibabaei et al. 2006), and the importance of using multiple independent character sets. However, this also highlights the utility of mtDNA in revealing cryptic hybridization, as recently shown by Linnen and Farrel (2007) in a study system with remarkable parralels to *Grammia*. Evidence for rampant mtDNA introgression among multiple species was not restricted to closely related species, challenging views that interspecific gene exchange occurs rarely and is restricted to recently diverged species.

In Chapter 4, phylogenetic analysis of *Grammia,* related genera, and representative genera of the subtribe Arctiina (in the broad sense) using morphology (81 characters), molecular data (658 bp of *cox1* mtDNA), and combined data partitions revealed moderate to strong support for monophyly of the two constituent subgenera of *Grammia*. Monophyly of *Grammia* was supported only by the morphology dataset, and monophyly of the subtribe Micrarctiina, which includes *Grammia* (Dubatolov 1996, 2003), was not supported. Phylogenetic placement of the genus *Virbia* Walker remains unresolved, and it is retained in the subtribe Arctiina following previous treatments. *Kodiosoma* Stretch is transferred from the subtribe Arctiina to the Phaegopterina. A revised subtribal classification of the North America genera previously placed in Arctiina (*s.l.*) is provided.

Several morphological synapomorphies supported the monophyly of the subtribes Spilosomina and Arctiina, comprising previous concepts of the Arctiina (Forbes 1960, Franclemont 1983, Ferguson 1985). This provides a starting point for future phylogenetic work on the basal groups within the large tribe Arctiini, and a step towards understanding the evolutionary history of complex mating and chemical ecology of tiger moths (Weller et al. 1999). Since phylogenetic characters consisted of morphological and molecular traits, a preliminary phylogeny should also shed light on the evolution of wing pattern in this distinctive group (Ferguson 1985). Molecular markers, such as the *EF-1a* and *wingless* gene of nuclear DNA, should be particularly informative for resolving deeper nodes within the Arctiini phylogeny, since these have proven useful at this phylogenetic level within the Noctuoidea (see e.g. Cho et al. 1995, Friedlander et al. 1994, Mitchell et al. 2006).

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Biography

Björn Christian Schmidt was born in Biedenkopf, Germany, and much of his early childhood was spent at or near his grandparents' farm in Rückershausen, North Rhine-Westphalia. His earliest entomological memory was that of finding the striking larva of an elephant hawk-moth (*Deilephila elpenor* [L.]) at age seven, which was promptly brought home in a pop can. He immigrated to Canada with his parents and three siblings in 1981 at age 9. The prairies and parklands surrounding Didsbury, Alberta were fertile grounds for exploration, and would be home until graduating high school. Weekend family trips to the mountains and summer trips to British Columbia were always greatly anticipated. Upon graduating high school in 1991, Chris enrolled in an undergraduate program at the University of Calgary, culminating in a bachelor's degree in Ecology in 1996. During the last year of this program, a summer position as a student intern at the Kananaskis Field Station gave Chris the opportunity to experience field work in a variety of ecology disciplines in the Rocky Mountain foothills, including work on *Parnassius* butterfly population ecology carried out by Jens Roland of the University of Alberta. It was this research that was particularly captivating, and a subsequent position as a research assistant in this and similar projects were followed by relocation to Edmonton. In 2001, Chris completed a three-year master's degree program at the University of Alberta with Jens Roland, which focused on forest tent caterpillar ecology. Prior to starting a doctoral degree program in 2004, Chris worked as a research technician and entomological consultant, and spent six months travelling in Ecuador. Chris completed his doctoral program with Felix Sperling at the University of Alberta in 2007, and is currently employed as an entomologist by the Canadian Food Inspection Agency. Ongoing interests and current projects include revisionary systematic work on the North American tiger moths and owlet moths. Chris lives in Ottawa, Ontario with his wife Margo Nelson and their two-year old son, Lucas.